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Vol. 94. 1944.

REVIEW OF THE CLASSIFICATION OF THE ARGYNNIDI: WITH A SYSTEMATIC REVISION OF THE GENUS *BOLORIA* (LEPIDOPTERA; NYMPHALIDAE)

By B. C. S. Warren.

Manuscript received 22 May, 1940.

(Read 3 November, 1943.)

With 46 Plates.

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For gifts of specimens I must thank Mr. F. T. Gilliat, Mr. P. Haig-Thomas, and the late Mr. E. C. Joy; the last, with that great generosity which was such a characteristic of his, also giving me his copy of Lang's *European Butterflies*, which he knew I needed for reference in connection with this work. To Drs. L. G. Higgins and T. Scott, D.S.O., I am indebted for the loan of specimens, with permission to dissect them. Many collectors do not realise how valuable even a few specimens may be to the systematic worker, if bearing accurate data. Dr. Higgins, who from his own extensive work fully appreciates this fact, was good enough to lend me nearly one hundred selected specimens from his collection, from localities ranging from Lapland to eastern China, and including topotypes of *B. pales palinoides*, which at that time I could not have obtained elsewhere. Mr. F. J. Griffin has, once more, done much to help in looking up references and descriptions, and Mr. A. M. Morley, O.B.E., has supplied valuable information on the derivation of certain names; while to Herr F. A. T. Reuss of Berlin I am indebted for separates, lists of references to his works, and numerous drawings illustrating and explaining his views. Especial thanks are due to Mr. Alexander B. Klots, of the College of the City of New York, for information in connection with North American races, and separates of some of his papers. The value of his help was enhanced by the fact that he has been working on the Argynnids of North America for very many years, with a view to producing a detailed account of *Clossiana* and allied genera. To Mr. Francis Hemming, C.M.G., C.B.E., I am indebted for many valuable suggestions, especially for his offer to check the references in my typescript; I only regret that it was impossible to give fuller data in connection with the distribution of the typical races of *Boloria pales* and *B. napaea*, as he wished; but I hope this work will enable the accurate identification of these races in future, and so lead to a more detailed knowledge of their distribution. Finally, I have to thank Captain N. D. Riley for adding proof-reading to his many other services; and, most especially, the Royal Entomological Society of London, not only for publishing the work, but for doing so under war-time conditions.

I. Introduction.

It was originally intended that this work should deal only with that group of the Argynnidi vaguely known as the "*pales* group." The need for some such work seemed obvious; the contradictory views and varying classifications employed by those who have had occasion to deal with the group must be familiar to all lepidopterists. At almost the very outset, however, it became apparent that no accurate estimation of the morphological data I was accumulating could be arrived at by an examination of this limited and rather generalised fragment of the great tribe of Argynnid insects; indeed from such a restricted field of research it was even questionable if one could hope to define the limits of the group itself with any certainty. A general survey of the morphology of the male genitalia of the Argynnids as a whole was therefore necessary before any real progress could be made. For many years past, work on such a survey had been carried out by F. A. T. Reuss of Berlin, who on the strength of his researches has formulated certain generic divisions of the tribe.

The Argynnidi as a whole (perhaps I should note that I do not include the Melitaeidi) present the most absolute generalisation of superficial character that can well be imagined, so far as the features of the upperside are concerned, a generalisation that gains in impressiveness as one recalls the numerical abundance of species and their almost world-wide geographical distribution.

It is this uniformity of facies that has led to the retention of the inclusive genus *Argynnis* for so long, in spite of growing doubts as to its real validity. The same cause will make the average collector incredulous, when he first hears that the generic divisions introduced by Reuss are not only essential to a scientific systematic study of the species of this great tribe, but that they still do not represent the last word on the subject. There is a strange unwillingness among many entomologists to allow systematic entomological work to follow scientific method in deed, instead of merely in supposition, and to this is to be attributed the almost complete disregard of Reuss's valuable work; but it must be admitted that Reuss himself rather gave those who wanted them excuses for continuing on the old lines and ignoring his efforts. The results of his work were published during the past twenty years or so, in short articles in numbers of different periodicals; some idea of the dissemination of his work can be gained from a glance at the list of references appended to this work; and it is not even a complete list. His habit of immediately publishing results as he arrived at them led to the necessity of frequent corrections on his part, and though he invariably corrected every inaccuracy, this greatly added to the difficulty of following his work. Yet another great detriment to the clear understanding of his papers was the lack of adequate illustration, and even the few illustrations he gave were, unfortunately, accompanied by many mistakes in their explanation. All these adverse circumstances made his work very difficult to follow, and speaking from my own experience, a wide, first-hand knowledge of the anatomy of the insects he dealt with was essential to a just appreciation of the value of his studies.

A simple exposition of Reuss's generic divisions is therefore the first necessity; and, as " seeing is believing," a full illustration of the structures on which he relied is also essential. To carry out this project to the full, on the Argynnids of the world, would have been an immense piece of work, and required many years to bring to a conclusion. I therefore decided to use the European species as a basis, as they would enable a sufficiently wide view of morphological character to be displayed, to demonstrate the accuracy of Reuss's work, and enable me to define the genera that include European species. It would then be possible to carry out the detailed study of the " *pales* group " that I had under consideration. This plan had the further advantages of both bringing before entomologists a true conception of the various very distinct genera now merged under the name *Argynnis*, with as little delay as possible, and providing a basis for the definition of the purely extra-European genera, at a later date. One may add that the latter would certainly be a greater task than the few genera indicated by Reuss might suggest, for the numbers of species in these genera are great, and a detailed study of them will almost certainly reveal the existence of genera at present unrecognised, the group-specialisation found among the European species being a tribal characteristic.

In this work I have relied solely on the structural characters of the male genitalia, which are so elaborate and constant as to make further characterisation superfluous. Reuss included details of the androconial scales, neuration, larvae, etc., in his definitions; but a lengthy study of these features, and his data relating to them, has shown that they are of insufficient constancy for generic definition, and are primarily of a specific nature, or, in certain cases it may be, indicative of smaller groups within the limits of a genus. To some extent, it seems to me, they may even have raised doubts as to the soundness of Reuss's conclusions in the minds of those who are not students of anatomy. It must also be noted that, with very rare exceptions, Reuss used in his definitions only the characteristics of the uncus, and though this process offers most valuable data, in the genital segments as a whole there are several other associated structures which provide even more impressive characters, such as the rudimentary gnathic processes, the phallobase, etc. The addition of such characters, corroborating as they do the testimony of the dorsal structures, supplies an absolutely irrefutable indication of the complete independence of the various groups of individuals (*i.e.* genera) within the tribe; this renders further characterisation superfluous.

I want especially to draw attention to the following point : in my revision of the genus *Boloria* I have, in general, made no mention of the many aberrations that have been given names. This is not an oversight. The *Boloria* species are prolific in aberrations, some of which are very remarkable, but such aberrations rarely, if ever, recur in exactly the same form; if the custom of giving names to such aberrations is continued, their number is bound to double every few years, if the work is accurately done. As only a minute fraction of these aberrations ever establish themselves as local forms, the cataloguing and describing of them is of no scientific value and from that point of view merely a waste of time. When an aberration is found to be constantly recurring in an appreciable proportion of the individuals of each generation, it can be accepted as a local form, and becomes worthy of description and a distinctive name : such forms are rare in *Boloria.*

II. OUTLINE OF THE MORPHOLOGY OF THE MALE GENITALIA IN THE ARGYNNIDI.

(*Note :* I am using the generic names for those divisions which the researches of Reuss and myself have shown to be necessary, from the outset; this will simplify the general continuity of the work, even if it seems strange to readers to start with. Full definitions of the European genera are given in part III; readers, however, if they follow this part carefully will get a far clearer idea of the isolated nature of the various genera, and the consequent impossibility of uniting them, than by merely reading the concise definitions.)

A brief explanation of the method employed in mounting the dissections that are described and figured in this work is necessary. Two things are essential in slides mounted for morphological study : (1) the possibility of obtaining clear photographs from them; (2) a certainty that all dissections will be uniformly displayed. It is not possible, when dealing with the Argynnids, to obtain these results by following either of the two most usually employed methods of mounting : *i.e.* displaying the genitalia in profile, complete, excepting that one of the claspers has been removed; or displaying the entire genitalia flattened out with the internal surfaces turned upwards. The latter method can give good results on occasions, as for example in the case of the specimen of *Proclossiana eunomia* (= *aphirape* (Hb.)) shown on pl. 12, fig. 43; but there is no certainty that the extensive folding of the 9th tergum, which is necessary, can always be accomplished in a uniform manner, so the production of really uniform mounts cannot be counted on. Further, in a very large number of other species, this method is absolutely impossible, owing to the great vertical development of the uncus, which obliges that process to be pressed to one side or the other, thereby distorting the whole of the central processes of the object, as well as forcing the uncus itself altogether out of place. The objections to the profile method are not quite so great, for it is always possible to make a serviceable mount by this method, such as is shown on pl. 4, fig. 10 (*Issoria lathonia*) or pl. 13, fig. 45

(*Boloria napaea*). But even so, the phallic organs are always more or less displaced, and often obscured to a considerable extent, so the method cannot be regarded as satisfactory. The best results were found to be obtained by removing the whole of the dorsal processes by detaching the 9th tergum at its point of junction with the coxosternal arc. This brings away the 9th tergum and all that there is of the 10th abdominal segment in one piece, which can be mounted in profile, thus displaying all the elaborate characters of these important structures to perfection. The remainder of the specimen, *i.e.* the claspers, vinculum and phallic organs, are then flattened out, so as to display the internal view of the claspers and the ventral view of the phallic organs. This gives a very excellent view of these structures, and there is a practical certainty that there will be perfect uniformity in all mounts made, for the process of dividing the specimen into these two sections necessitates the cutting and removal of certain portions of the internal membrane, which permits the necessary freedom of movement to the various parts. It follows that, with but little difficulty, the dissections can be brought into the required position, with all parts on an approximately uniform plane, which ensures that every organ is so displayed that any photographs required can be made.

In just a few species where the uncus assumes very exceptional formations, it has been necessary to mount some of the specimens with the dorsal parts flattened out so as to show their internal surface, as well as others in profile; this permitted photographs of both aspects to be made.

Among the species of the Argynnidi one finds in the male genitalia a wealth of elaboration in structural detail such as I have not found among the members of any other tribe of butterflies that I studied. No process, no matter of how simple a character in some species, is wholly free from this elaboration in others. Reuss (1922c) regards much of this highly complicated elaboration of simple form as the outcome of uncontrolled variation; and in certain cases simply as a luxurious and valueless superfluity. I will have to refer to this point again, but I cannot agree with the suggestion that much of this elaboration in development is purely superfluous, for there are clear indications that it is a tribal characteristic in the Argynnids of very considerable antiquity, which specialisation has been able to exploit to the utmost. Thus we find most elaborately specialised formations common to a number (sometimes a large number) of different species having an immense range in geographical distribution, such as throughout Europe, Asia and North America; yet they remain absolutely constant, in spite of an ever-present tendency to individual variation. The existence of many such groups shows the great antiquity of this elaboration of structural form, as well as the absence of any close affinity between the various groups; for it appears quite impossible to suppose that such uniformity of structural specialisation could have been arrived at independently by a number of species now ranging throughout the Holarctic Region. One must therefore assume the specialised formation to have been fully developed in some common ancestor of each group, the ensuing multiplication of species and their wide dissemination merely increasing the group without modification of its specialised nature. A little consideration of these facts helps the realisation of how widely separated these Argynnid genera are in time, and how little significance there attaches to the common coloration and pattern of the upperside of the insects.

The following discussion on the nature and characteristics of the male armature in the Argynnidi is mainly based on the European species, so far as my own researches go, together with such data as Reuss's work supplies on the extra-European species. In these two sources, however, I feel reasonably satisfied that we have a sufficiently detailed and accurate material to establish the main morphological characteristics of the tribe.

On starting any examination of the Argynnid male genitalia two characters at once claim attention, for they are (so far as Reuss's and my own researches have gone) both common to all species of Argynnids and peculiar to them: (1) the presence of a non-chitinised area in the dorsal region of the 9th tergum, and (2) the fact that the terminal (distal) process of the harpe lies external to the clasper, instead of being located either internally (most usual in other families) or in a dorsal extension on a common plane with it.

This terminal head of the harpe is a most important feature, and owing to the necessity for constantly referring to it, some name for it is essential. Reuss (1921b and 1922a) refers to it together with the terminal, dorsal extremity of the clasper, as " obere und untere flagellen "; or, simply, as " valvenflagellen," on account of his observations on the use and motion of the claspers. I cannot, however, feel certain that he has interpreted his observations correctly. He has recorded that during copulation the claspers maintain a lateral motion, tapping on the body of the female and not retaining a fixed grip. I, too, have on occasions noted this sort of vibration of the claspers in other species, but it did not suggest to me a real relaxation of grip, or that the claspers were merely used for whatever purpose this motion may serve, and not for definite grip as well. I cannot, therefore, accept his inference when he states (1922c : 366) : " Wenn der Unkus beim Männchen und die Vermicula bei dem Weibchen aktionsfähig waren, dann brauchten die Valven überhaupt nur dabei zu sein in irgendeiner Form." In spite of the vibration in actual use, I feel the extraordinarily varied clasper formations are not wholly fortuitous; especially when, as I have already pointed out, given formations of a most specialised nature appear in a number of distinct species of wide geographical distribution, and yet remain absolutely constant within the limits of the group. Again, the terminal process of the harpe, indeed the entire harpe, is very distinct from the dorsal terminal process of the clasper; to describe these two processes as the " upper " and " lower " seems to me to convey the mistaken and misleading suggestion of unity. For these reasons I do not adopt the names Reuss used; but shall call the free, distal termination of the harpe simply the " head " of the harpe. The harpe and its developments is dealt with in detail later (see pp. 16–20).

The unchitinised, membranous area, common to all Argynnids, and located in a central position in the 9th tergum, can best be illustrated in those species in which it is possible to mount the 9th tergum and uncus flattened out and viewed on the inner surface (see pl. 4, fig. 11; pl. 9, figs. 26, 27, 30; pl. 22, figs. 103, 104, etc.), but it can also be seen in every profile photograph of the uncus, and in many of these the dorsal line of the membrane that covers the cavity can be distinguished. Although, normally, this membranous area is confined to the 9th segment, on occasions it extends into the 10th, as in *Brenthis hecate* (pl. 8, fig. 24, and pl. 9, fig. 26) and *B. daphne* (pl. 8, fig. 25, and pl. 9, fig. 27). In these species the membranous area is somewhat arrow-shaped, the head of the arrow being formed by the non-chitinised area in the base of the 10th tergum. This is a comparatively rare occurrence, only seen in a few other species; in the great majority of species the uncus is completely chitinised, and the membranous area more triangular in shape, as in figs. 103 and 104.

As already noted, this membranous area and the external position of the distal extremity of the harpe, are developments peculiar to the Argynnids, and they separate that tribe very sharply from the Melitaeidi. I do not know if any such loss of chitinisation occurs in other NYMPHALIDAE, but in many of those species of SATYRIDAE which have developed the curious clusters of chitinous rods, usually referred to by the misleading name of the "Jullien organ," we find an analogous loss of chitinisation in the 8th tergum; for the rods are appended to the tergites of the 8th segment. In some cases, however, the distal extremities of the tergites reunite dorsally, and then we get an enclosed membranous area much more resembling that seen in the Argynnids, and in such cases it might be correct to say that the rods were articulated on the 8th tergum. In either case, the fact that the rods, and often much of the foundation from which they originate, overlie the 9th tergum more or less completely, gives considerable ground for supposing there may be more analogy between this membranous area in the Satyrids and that in the Argynnids than would seem likely when one thinks of them only as located in different segments. That these non-chitinised areas are connected in no small degree with the use of the uncus in the Argynnidi, is suggested by Reuss's observations on the movement of the latter (1922a, 1927, etc.), and supported by his notes on the SATYRIDAE (1927); but before we examine this idea it will be necessary to consider the morphology of the uncus in detail.

In the 10th tergum, or uncus, we come on the first examples of those immense capabilities for elaboration of the most simple structure, that are inherent in the Argynnids. In *Argynnis paphia* the uncus is long and of no great depth, abruptly bent at almost a right angle, near the base, at the point of union of the two lateral edges; from this point it tapers rapidly to its extremity, terminating in a hooked tip with a sharp point directed ventrally. Just at the right-angle bend a thin, vertical, fin-like crest rises from the dorsal ridge; from this crest spring several strong prongs, of varying size and number, directed distad. Two examples of this remarkable uncus are shown (pl. 1, figs. 2 and 3), and when one recalls that the movement of the uncus is downward, enabling the point to secure a hold, the array of prongs on the dorsal ridge at first appears entirely useless. But Reuss's observations have shown that this is not the case, and it is a warning against a too hasty conclusion that seemingly useless elaboration must, necessarily, be so. A further elaboration of a somewhat similar type is seen in *Pandoriana pandora* (pl. 2, figs. 5, 6, and 7). Here, however, the uncus is far shorter, deeper, and a sharp terminal tooth replaces the hooked tip. From the dorsal ridge rises a thin, vertical crest, homologous to that of the *A. paphia* uncus, but much deeper, and usually bearing a greater number of shorter prongs; the number varies considerably. Reuss (1922a) gives the number in *A. paphia* as four to six; in *P. pandora* as six to eight. It will be noted that fig. 7 shows no fewer than ten of these prongs. With respect to their use, Reuss, from his observations on paired insects, states that the hook or tooth at the tip of the uncus engages an organ of the female that he calls the "vermicula" (1922a), which lies dorsal to the vagina to which it may be attached as in *Mesoacidalia charlotta* (= *aglaja* (L.)) or *Fabriciana niobe*, etc.; or free from it as in *Argynnis paphia*. When the hook is secure in the vermicula the uncus is folded completely over, so that the ridge prongs are all brought into contact with the vermicula also, and fasten into it. The grip obtained in this manner must be very tenacious; the presence of the ridge prongs in the male always coincides with the presence of the vermicula in the female; but among the European species this combination is known to occur only among the larger species. It is of interest to recall here, that among these large species the flight habit when paired differs from that prevailing among the remaining (European) species of the tribe, in that both sexes can fly at will. Among the smaller species one sex only, the female, is known to fly during copulation. The development of this abnormal flight-habit appears, therefore, directly correlated with the presence of the dorsal prongs in the male and the vermicula in the female.

In *Fabriciana* (pl. 6, figs. 15, 16, 17) the uncus is of very different form, very deep to start with, then tapering gradually to its extremity and terminating in a very small, sharp point, bent downwards at almost a right angle. The whole uncus is curved, the ventral outline being deeply concave with a sharp, angular excrescence at about half its length, at the point where the two lateral edges unite, beyond which (distad) the uncus is sealed ventrally. From the dorsal ridge, at a little distad from the position of the ventral angle, rises a thin, fin-like, vertical crest; the ridge of this crest is jagged. These jagged points represent the armament of prongs of *Argynnis paphia* and *Pandoriana pandora*, and doubtless serve the same purpose. The vertical expansion of the crest varies according to the species; it may be considerable as in *F. adippe* (fig. 17), very slight as in *F. elisa* (fig. 16), or wanting as in the Indian species *F. kamala* (not figured), but the jagged edge always persists. This is produced by a series of very small excrescences on the ridge of the crest, when present, or on the actual ridge of the uncus when there is no crest. These excrescences are just sufficiently prominent to break the even dorsal outline, though slightly more developed in some individuals and less in others. In some specimens of *F. kamala* they are so fine as to require considerable magnification to make them visible; at least eighty or one hundred diameters. When the crest is prominent it gives the false impression that there is an abrupt change in depth of the uncus immediately distad of the crest; but in reality the uncus tapers gradually from the point of greatest depth, just proximad of the crest, to the termination; the true form is an even curve, such as one sees in *F. kamala*, which can be seen with oblique illumination under the microscope even when the crest is present, in other species. It is worth noting that in *F. kamala* there is a supplementary series of extremely fine excrescences on the ventral edge of the uncus immediately before the terminal point, a feature which also occurs in some individuals of other species, but it too can only be observed under greater magnification than is normally necessary.

In *Mesoacidalia charlotta* (= *aglaja* (L.)) we find yet another uncus of the dorsally armed type (pl. 6, figs. 19, 20). Similar at its proximal end to those last described (*Fabriciana*) it retains its full depth over the entire length, the dorsal ridge being produced to form the small, sharp, terminal hook, overhanging the ventral edge, which is rounded off. The vertical crest of the dorsal ridge is not very pronounced, but extends over a greater area of the uncus than in *Fabriciana*, in a gentle curve; the ridge is jagged. There is much variation in the coarseness or fineness of the excrescences, as can be seen in figs. 19 and 20; the ventral angle at the point of union of the lateral edges is nearer the base than in *Fabriciana*.

The uncus in *Issoria lathonia* (pl. 4, figs. 10, 11, 12) is a structure of extreme simplicity; quite short, slightly curved and tapering a little towards the tip, which bears minute teeth that are scarcely visible even under the higher magnification in fig. 11. The chief point of interest attaching to the uncus is the small, dorsal prominence, at the junction of the uncus and the 9th tergum. This blunt point might well pass unnoticed; but it is worth attention, for in this species the vermicula is modified and not extensible (Reuss 1927), as in the other species. This blunt, dorsal point on the male uncus may therefore be a rudiment of a lost dorsal armament, or more probably one that was never further developed; for the sternal processes of the 10th segment are most extremely specialised, as we shall see later, and this sternal elaboration probably interfered with the fuller development of the dorsal processes, which the modified vermicula in the female organs suggests might otherwise have been possible. The reason for supposing the sternal elaboration to have obstructed the development of the external dorsal armament is perhaps not immediately obvious, but I have already noted that, to bring this external armament into use, the uncus must be capable of being completely folded over on itself. Reuss (1927) estimates that the arc of movement of the Argynnid uncus is at least 180°—which, on looking at the photographs on pl. 4, will be seen to be quite impossible of attainment owing to the position of the sternal processes, and as these processes are attached latero-ventrally to the proximal aspect of the harpe, as well as dorsally to the tergum, they are incapable of any material displacement.

I have already pointed out, when referring to the non-sclerotised area of the 9th tergum, that this movement of the uncus in use may in no little degree be correlated with the absence of sclerotisation in that area, and that Reuss's observations on the range of uncal movement support this view. There is no question that the membranous area permits the necessary lateral expansion of the distal end of the 9th tergum, as well as to a certain extent facilitating the downward curving of the uncus. Reuss (1927) estimated that in the SATYRIDAE the uncus has an arc of movement of only about 90°, *i.e.*, only half that of which the Argynnid uncus is capable. The necessary amount of give and displacement in the dorsal region of the Satyrid structures could, therefore, be obtained from an area more remote from the base of the uncus than would be required in the Argynnidi. This suggests that the membranous area in the 8th tergum in the Satyrid structure is actually analogous to that in the 9th tergum of the Argynnidi, in spite of the difference of position. The fact that the 8th abdominal segment in the male is rarely mentioned in connection with studies of the genitalia by lepidopterists does not affect the inferences just drawn though, perhaps, it may be accepted as intimating that this segment has no real connection with the genitalia of the male lepidopterous insect. That, however, is not the case; we are reminded by Snodgrass (1935) that the 8th segment forms " at least a protractile base for the copulatory apparatus," a service in the operation of which the uses of the membranous area must be fully drawn upon.

Five other distinct types of uncal formation must be mentioned. That shown on pl. 3, fig. 9, is a strangely specialised form, found only in one European species, *Argyronome laodice.* The terminal hooked tip is similar to that seen in *Argynnis paphia*; what the merit may be of the curious upward slant, from just about the region where in most other species the change of direction is downward, is difficult to imagine.

Then we come to what looks at first sight like a very simple and usual type of uncus; especially if it is viewed only in profile. When it is flattened out, however, and viewed on its internal or external surface, a small but very remarkable character can be noted. The uncus has the appearance of having a bifid distal extremity, such as is frequently found in other Argynnids, and species of many other families. But between the double terminal prongs there is a third very small prong, so that the extremity is actually trifid. This peculiarity is known in only three species: *Brenthis hecate, B. daphne* and *B. ino* (pl. 8, figs. 24, 25, and pl. 9, figs. 26, 27, 29 and 30). The central prong is best seen in the ventrally expanded uncus, and the more highly magnified photographs; it can only rarely be observed in profile: fig. 29 is an exceptional mount that permits all three prongs to be seen in that position. So far as I can ascertain, this trifid termination of the uncus is unknown in any other species of European butterfly, and I have come on no reference to it in such works on Asiatic or American insects as I have consulted.

Next, we have a simple type of uncus, short, deep in proportion to its length, slightly curved, with a bifid tip. This is the type of the genus *Clossiana*, which includes a large number of species; examples of these are given on pl. 10, figs. 31, 32; pl. 11, figs. 36, 38, 39, 40; pl. 12, figs. 41 and 42. It is necessary to refer to one species in detail: *C. selene*, the genotype. Of this insect, Reuss (1921b) asserts that the uncus is divided longitudinally into two portions, instead of merely having a bifid tip. He returns to this point more than once, and in a later paper (1922a) wrote the following in a footnote to p. 226: "Der Uncus ist am lebenden Tier sehr beweglich und teilt sich bei *selene* in zwei getrennt bewegliche Hälften. In der Ruhestellung klaffen nur die Spitzen auseinander und der Uncus sieht nicht anders aus als ein unteilbarer." In yet another footnote in the same paper (p. 228) he adds that the division of the uncus can only be observed while the insect is alive. This is one of the few cases where I find Reuss's observations at fault. From the minute examination of a couple of dozen specimens, I can only attribute Reuss's misapprehension either to a quite abnormal specimen in which the uncus was divided, or to the possibility that alternate lateral movements of the uncus in a living specimen gave him a false impression that it was divided. As to the first possibility, I have no evidence that such specimens ever occur, but in all those species in which the uncus is at all deeply bifid, it is easy to split it by too great pressure in mounting a specimen. Some combination of such an accident, and a mistaken observation of the actual range of movement in a living specimen, must have misled Reuss; for in every specimen I dissected the uncus proved to be a single, indivisible structure. When spread out flat and mounted as shown in fig. 42 (pl. 12) and examined under considerable magnification, the central area of the uncus is seen to be less heavily chitinised than the sides; but there is not the slightest trace of any fissure or break in the uniform chitinous surface. Fig. 42 is magnified fifty times and shows the continuity of the chitinisation clearly. I have examined specimens under much higher powers with the same result. The uncus may be very flexible and capable of considerable movement, but if a specimen is found in which the uncus is indeed in two separate parts, it seems certain that such a condition must be completely abnormal, probably pathological. In the course of my researches I have come on many kinds of malformation affecting the uncus, and not a few (in several species) in which the uncus is doubled up under the 9th tergum. To such a category must a divided uncus belong, if it were found.

There remain two less striking types of uncal formation to note. One of these, peculiar to the genus *Proclossiana* (pl. 12, figs. 43, 44), is very specialised, though not elaborate. This uncus is short, very slender, tapering to a fine point, the actual tip of which is bifid and slightly curved downwards. The cleft in the tip of this uncus is shallower than in any other type of bifid uncus. The second form, found in the genus *Boloria*, is also simple (pl. 13, fig. 45; pl. 24, figs. 112, 116, 117; pl. 22, figs. 103, 104, etc.). This uncus is the shortest known type, but much broader and deeper than the *Proclossiana* type, in proportion to the length. It is slightly curved and much more deeply bifid at the tip, where two small, terminal prongs are developed.

Before leaving the features of the uncus it is well to note that the two sclerites of the tegumen and uncus, which can be seen in most of the illustrations looking like appendages of the 9th tergum, belong to the 10th segment and may be homologues of the laterotergites of Snodgrass. Though in the photographs these pieces look quite detached from the proximal base of the uncus, they are actually one with it on each side, the visible gap being caused by a short, connecting portion which is not chitinised. These details can best be seen in figs. 2 and 3, pl. 1; fig. 9, pl. 3; fig. 12, pl. 4; and less clearly in many others. At the proximal end of the laterotergites in some species, remnants of a further portion of the sides of the 10th segment exist, but this is unusual. These remnants are best developed in *Argyronome laodice* (pl. 3, fig. 9), they terminate at the junction with the coxosternal arc of the 9th segment. At this point, however, one finds in some species two chitinous plates, that connect with the sternal ends of the 9th tergum and the proximal end of the harpes. Various views of these plates are shown on pl. 6. That they are rudiments of some form of gnathus and represent the sternum of the 10th segment, there can be no question. Owing to their location on a plane at right angles to the vinculum and parallel to the tegumen, profile mounts of the dorsal structures show these plates forced up on edge, as in figs. 15, 16, 17 and 20. The nearest approach to their normal position that can be achieved in a mount is produced by cutting away the uncus and distal half of the tegumen, and all that there is below the plates, and then placing them flat on the slide, folding down the remaining portion of the tegumen to which they are attached, as shown in fig. 18. The plates are thin, featureless chitin, and normally lie with their internal edges overlapping about as much as is shown in fig. 18; the overlapping edges, however, are those which are *uppermost* in the photograph. It will be seen that there is a small piece torn out of the lower inner corner of each plate. This is the result of detaching them from the harpe, which unfortunately also permits them to slue round. If these corners were still attached, the flat edges of each plate, between the two points of contact (*i.e.* the two corners), would be flush with the vinculum on each side, and therefore parallel to each other. The rounded edges seen uppermost in the photograph would then be innermost, and overlapping. When the uncus is bent down, in the manner already described, so as to enable a grip to be obtained with the dorsal serrations or prongs, the plates slide apart, horizontally, in response to the expansion of the tegumen; with the return of the latter to a normal state, the plates slide together again. In other families the gnathus is represented by a single process, in which there is no ventral division. Among the Argynnidi, in a few species where a more complete gnathic structure exists, this consists of a single piece, also without any ventral division. These facts make the evolution of the plates, with their capacity for horizontal movement, all the more remarkable. This horizontal action enables adjustment, exactly proportional to the strain on the tegumen at any moment, to be achieved without resorting to a direct, permanent, ventral opening. Indeed, it seems probable that the extent to which the plates overlap, which of course would permit expansion equivalent to that amount, is sufficient to meet the greatest strain and maximum motion of the uncus without actual separation, so that even a temporary removal of the ventral plate is avoided.

The gnathic plates are present in the genera *Fabriciana*, *Mesoacidalia*, *Argynnis* and *Pandoriana*, and possibly in some non-European genera also. In *Argynnis* they are least developed.

The most highly developed gnathic structure in the Argynnidi is found in *Issoria*. A glance at fig. 12, pl. 4, will give a good idea of this process, which consists of a strongly chitinised ventral plate with upward-curving sides, from the dorso-distal aspect of which rise two side pieces, extending towards the tegumen. The whole process is studded, externally, with fine but strong points; it connects with the ventral edges of the uncus by two lightly chitinised curved bands, clearly seen in fig. 10, where they are superimposed on each other and consequently look denser than in reality. In the proximal area the connection of the gnathus is mainly a membranous union with the internal membrane; but there is a slightly chitinised connection with the extreme ventral point of the tegumen. This connecting piece was lost in dissecting the specimen shown in fig. 12. It is strange that this remarkable structure has so rarely been referred to in the past. Petersen (1904) suggested it might be a scaphium, but Reuss (1922a) observes that that suggestion was certainly incorrect, though owing to its rudimentary nature he questions if it might not be called a " subscaphium." In my opinion, it seems to be less rudimentary than Reuss supposed, for with but a slight increase of chitinisation in the region of the latero-dorsal connecting bands, one would have an abnormally well-developed 10th segment. The great difference between this and the only other gnathic structures known in the Argynnidi (the plates just described in *Fabriciana*, etc.) further emphasises the relatively high degree of development represented by this remarkable structure. I have previously noted that specialisation in this gnathus may have been detrimental to the development of external armament on the dorsal ridge of the uncus in this species, through obstructing the vertical range of movement of the latter. A purely rudimentary gnathic process could not have been an effective obstruction; and the presence of the vermicula in the female organs, as well as its more simple form, both point to some check to development having taken place. Reuss states (1922a) that a similar gnathus is present in the African species of *Issoria gemmata* Butl., etc.

I may perhaps add that the name " gnathus " was chosen by Chapman and first published by him (1911); he wrote it as given here, doubtless with the intention of keeping the name uniform with the many other names attaching to associated structures that terminate in like manner.

We now come to the phallic organs. The aedeagus and phallobase show remarkable variety in form; the latter, with its associated processes, being least known and of greatest interest, I shall deal with first. The true basal plate of the phallobase can scarcely be said to exist, as such, in the Argynnidi. It is represented by an insignificant somewhat triangular sclerite located in the membrane ventrad from the aedeagus. From this vestigial plate spring twin processes, which support the aedeagus in fault of a more normal sheath, which does not exist. These twin processes assume an amazing variety of forms, ranging from a pair of simple strips of featureless chitin, to structures of great elaboration and beauty. The simplest form closely resembles the winged seed-pod of some plant (see pl. 23, figs. 105, 110; pl. 25, figs. 121, 122). They are seen in these figures, located centrally between the two claspers, the aedeagus having been removed so as to give a clear view; they can be recognised in most other photographs superimposed on the aedeagus. I propose calling these twin processes the " wings " of the phallobase.

The simple form of the wings prevails in the genus *Boloria*, the species of which constitute the " *pales* group " as most generally understood. This form reappears, on a slightly larger scale, in *Proclossiana eunomia* Esp. (= *aphirape* (Hb.)), where the distal expansion of the wings is markedly greater (pl. 12, fig. 43). Further developments of this type are found in *Brenthis* (pl. 8, figs. 24, 25) and *Clossiana* (pl. 10, figs. 31, 34, and pl. 11, figs. 35, 37). In *Brenthis* the wings are slightly longer and narrower, and taper distinctly to their distal extremities, instead of expanding; while in *Clossiana* they are longer and rounded off without any change in width. Again, in *Mesoacidalia charlotta* (= *aglaja* (L.)), we find the latter type (pl. 7, fig. 22), the wings being no larger than in *C. titania* in spite of the much greater size of the insect. In *Issoria* there is a form somewhat similar to that of *Brenthis*, on a larger scale; the wings are a little broader at their base, are decidedly longer, and taper to finer points (pl. 4, fig. 10). Among some of the largest species a simple form also occurs, but more specialised, and on an immensely larger scale. In *Argynnis paphia* (pl. 1, fig. 1) the wings are triangular, the apex of the triangle turned towards the base, the distal termination broad and flat. It is difficult to make the wings out in fig. 1, as they are invisible against the very dense aedeagus and only such parts of them as project beyond it can be seen. To the left, the flat, distal end of one wing shows, and a part of the other on the right; from these portions, however, it is possible to gather an idea of their size and shape. In *Pandoriana pandora* the wings are about the same dimensions as in *A. paphia*, but differ considerably in shape, being remarkable in that they are nearly their full width at their base, and contract towards their extremity only to expand again to a greater width than before (pl. 2, fig. 4). They are therefore very specialised in nature, though having an appearance of extreme simplicity of form. In fig. 4, the wings are seen separated and pushed to either side of the uncus.

There remain two other types to consider, both extremely specialised. Of these, in *Argyronome laodice* (pl. 3, fig. 8) the wings are far larger than in *P. pandora*, although the former is not so large an insect. The wings are restricted at the base, and broaden out continuously to the distal extremity, where they are folded over on themselves, producing a terminal fold of double thickness. They are of far greater dimensions than in any other European Argynnid, also more widely separated at their base, the basal plate being broader; the terminal fold is unique. The massive development is obviously necessary to support the immense aedeagus, which almost equals the claspers in size.

Finally, in the genus *Fabriciana* we find the most specialised form of all. The basal plate is slightly more developed than is usual, and extends proximad a short way from the point of origin of the wings; the latter are narrow, slightly rounded, and extend distad in graceful curves. The combination of these features gives the whole process a beautiful, lyre-like appearance (pl. 5, figs. 13, 14; pl. 7, fig. 21). The wings are composed of double layers of chitin and are slightly rounded, each terminates in a sharp beak-like point (best shown in fig. 21), and has a fin-like projection located latero-ventrally at about half its length. These " fins " are always present, though not seen in fig. 13. Their position on a slightly rounded surface renders them liable to assume varying positions in mounted specimens, as the result of pressure. Although there is a specific modification of form in these wings in each species, the type remains unaltered, in spite of the wide range of the species of this genus.

There is, as is natural, a close connection between the developments in phallobasic structure and the aedeagus; so we find the simplest type of the latter correlated with the simplest type of the wings of the phallobase, in the genus *Boloria*. The aedeagus in this group of species (see pls. 13–29) is a featureless, chitinous tube, larger in proportion to the size of the claspers than in many other genera, broad in proportion to its length, tapering slightly to the distal, and more markedly to the proximal end. The endophallic tube carries an armament of small, pointed, chitinous scales, the points directed distad, internally, but proximad when the tube is everted. These scale sheets are seen as two black patches on each side of the membrane in most of the photographs; a third patch situated centrally, below (as seen in the photographs) the two external patches, is the remainder of the scales which are still in their internal situation. These details can be clearly seen in figs. 51 and 52, on pl. 14, and in many others.

Between this simple type and the next there is a considerable change, the organ becoming narrower in proportion to its length, broader at the base, and tapering continuously to a point at the distal extremity; the scale armament of the endophallic tube is of a slightly coarser nature. This type is found in *Issoria*; it cannot be seen in the photograph of *I. lathonia*, pl. 4, fig. 10, which was selected to show the remarkable gnathus in relation to the whole genitalia. Next there is another simple form (*Proclossiana*, pl. 12, fig. 43) in shape more like the first type (*Boloria*), a narrow tube at the base but broadening abruptly in the middle, then contracting again; it is slighter on the whole, and the chitinous scales of the endophallic tube are finer, appearing more abundant owing to the more voluminous proportions of the membrane. A further development of the endophallus, in the same direction, is present in the next type (*Brenthis*, pl. 8, figs. 24, 25). The everted membrane spreads in broad folds on either side of the narrow, ventral strip, which is all that remains of the chitinised wall of the aedeagus in the distal half. This narrow end of the aedeagus can be clearly seen in fig. 25, pointing upward (as it appears in the photograph), the broad featureless proximal half underlying the wings of the phallobase. To the left of the narrow extremity, curve the bulging folds of the endophallus, densely clothed with minute pointed chitinous scales. At the edges of the folds these scales are coarser, constituting a more or less inflexible rim, which always remains external to the aedeagus. This type is transitional to the next, which is extremely specialised, though common to a large number of species (*Clossiana*). In view of its remarkable features, I have given two more highly magnified photographs, illustrating the lateral and ventral views of this aedeagus (pl. 10, figs. 33, 34). These photographs show the chitinisation of the aedeagus to be still more reduced than in *Brenthis*; the proximal end of the tube is extremely narrow to start with, and only complete over a limited area close to the base, the dorsal area being unchitinised for about two-thirds of the length before the centre, where the tube is again entire and attains its greatest expansion. From here it is reduced abruptly to a narrow ventral plate, the dorsal area being occupied by the elaborate convolutions of the endophallus, the flap-like lateral folds of which are similar to those existing in *Brenthis*, but much more developed and the outer rims more strongly chitinised over a considerable area. The proximal ends of these rims connect with a series of very strong chitinous teeth located internally in the endophallus. When this portion of the membrane becomes everted, these teeth form a most striking rosette on the dorsal surface of the membrane (pl. 10, fig. 33 external, fig. 34 internal position). It is well to remember that this aedeagus is actually only slightly larger than the *Brenthis* type; the enlarged photographs are apt to convey an idea of greater dimensions. The figs. 31 (pl. 10) and 35 (pl. 11) show the aedeagus at the same magnification as in the photographs of the other species. There are, as usual, many slight deviations in form and extent of development to be found in this type of aedeagus among the many species of the genus *Clossiana*: the extent of chitinisation of the membrane, and the size of the teeth, are two characters that are especially liable to be affected. In some species, such as *C. thore* (pl. 11, fig. 37), the organ might be said to form a transition to the *Brenthis* type; but the form of the proximal half of the aedeagal tube shows that it is a variant of the more specialised *Clossiana* type. One may next take the type of the genus *Fabriciana*. The aedeagal tube is broad at the base, almost its full width, and more extensively chitinised than in the *Brenthis* type. The whole outline is fairly uniform, though chitinisation is still strongly reduced distally. The endophallus is still very ample, but does not develop the flap-like distal expansions. It carries a dense clothing of extremely fine chitinous scales, and a central cluster of strong teeth (pl. 5, figs. 13, 14; pl. 7, fig. 21). This is the first type in which the endophallic armament of teeth is permanently external, either partially so, as in this type, or nearly completely so, as in others. The next stage in the development of these endophallic teeth is found in *Mesoacidalia charlotta* (= *aglaja* (L.)) (pl. 7, figs. 22, 23). Here the aedeagus is shorter and very simple, but very broad centrally, the width being but little less than the length. The endophallic tube is as long as in the last type, and very densely clothed with strong teeth, in the central area; these teeth partially replace the wall of the tube of the aedeagus (seen as a black mass in the photograph) while the distal, eversible portion, is completely covered with fine scales.

There remain three other types, all extremely specialised. That of *Pandoriana pandora* (pl. 2, fig. 4) is nearest to the last, but differs in being long and narrow. The distal quarter of the endophallus bears a dense mass of coarse teeth, for the greater part external; only a very limited portion bears scales, and is eversible. The two remaining types are the most striking of all. In *Argyronome laodice* (pl. 3, fig. 8) the aedeagus is of gigantic proportions, unapproached in any other species that I have examined. As can be seen in the photograph, in size the aedeagus is as long as the claspers and but little narrower. The proximal end is a very perfect representation of a fish's tail; in the distal half the chitinisation of the tube is wanting dorsally, and replaced by an endophallic armament of teeth that range from great spines to quite short teeth, but all of a coarse nature, and practically all external. In contradistinction to the immense development of the phallic organs is the very slender uncus (fig. 9), which looks altogether disproportionate. In *Pandoriana pandora* the position is exactly reversed, the uncus being very strikingly large, and the phallic processes reduced (pl. 2). Lastly, in *Argynnis paphia* we find another extremely specialised type. The aedeagus is of more normal size, in proportion to the periphallic and dorsal processes, but the chitinisation of the wall of the aedeagus might almost be described as fragmentary. Fully seven-eighths of the laterodorsal area of the wall of the aedeagal tube are replaced by the spinal armament of the endophallus. The great density and number of these spines can be realised by a glance at pl. 1, fig. 1, where they have the appearance of being a solid, opaque body. This mass, however, is entirely composed of separate spines, the points of which can be seen, directed distad, up the right-hand edge of the organ, in the photograph. It will then be noted that at the left-hand edge, near the top, the direction of the spines is proximad. This fact is of great interest, for it at once suggests that the terminal " head " of the aedeagus is eversible; hence the reversal of the spines. But in fact this is not the case. The " head " and the main body of the spines are one, in that the main mass, without any alteration in direction on the part of the spines, always attains the extreme end of the organ. If one follows them up both sides of the spine mass shown in fig. 1, they will be seen to run together to a point at the extremity, and on this particular little area of the terminal " head " the spines are still directed distad. Over all the rest of the " head " they are directed proximad. There is, however, no real division between the two zones of spinal orientation. This, together with the fact that in the small sector the direction of the spines never changes to the absolute extremity, proves that the changed orientation of the majority of the spines in the terminal area cannot be accounted for by eversion. Whatever brought about this change, one cannot doubt that the reversal of direction serves the same purpose that spines normally brought into this position by eversion would serve.

Down the left-hand edge of the aedeagus in fig. 1 will be seen a narrow dark object. This is a cylindrical thickening of the free edge of the aedeagal wall, and not connected with the spine mass, as might be thought from the photograph. This curious process is studded all over with short strong spikes. It may be added, that though the spine mass is external, and very solid, the spines are completely free from each other; they originate from a membranous surface. There appears to be no exact uniformity in different specimens, of the extent to which the points of these spines are raised above the surface, which suggests that this depends on pressure in mounting, and that they can be raised or lowered at will.

There now remain the claspers and saccus to be reviewed. The latter, though varying in size, is otherwise featureless; it calls for no comment. The claspers, on the other hand, display an extraordinary diversity of form and development; but as already noted in connection with the other organs, these developments tend to produce types peculiar to certain groups of species.

In studying the claspers, three main centres of development must be recognised: (1) the harpe; (2) the distal extremity of the clasper as distinct from the harpe; and (3) the internal developments relating to the dorsal edge of the clasper. Of these, the harpe is the most elaborate and important. I have already noted that the external position of its distal extremity is a remarkable (possibly unique) characteristic of the Argynnidi. Before going further, therefore, it is well to note the general features of this process. The harpe lies along the dorsal edge of the clasper and consists of an internal, proximal portion, and an external, distal portion, united by a more or less featureless central section. The distal portion is subject to the greatest elaboration in form: the proximal usually forked; the dorsal branch simple, connecting with the gnathic rudiments, when present, or the vinculum; the ventral branch more elaborate (but sometimes wanting) connecting with an excrescence on the outer chitinous wall of the clasper not far from the base. Unlike the harpe as it exists in many other tribes, the harpe of the Argynnidi is composed of a double layer of chitin, derived from both the inner and outer walls of the clasper. On pl. 1, fig. 1, the harpe can be seen to advantage, the dark head with its covering of strong short teeth lying external to the terminal prongs of the clasper (*i.e.* under it in the photograph), while the proximal fork overlies the clasper on its inner side. Both parts can here be recognised as components of a single indivisible piece, only united with the dorsal ridge of the main body of the clasper by a short span of the outer chitinous sheet. It will be recognised, then, that the forked prong at the dorso-distal apex of the clasper is a development of the latter, and is not attached to the harpe. To unite this prong and the head of the harpe under one name, as the "upper" and "lower" aspects of one unit, as Reuss has done, is a misconception of the nature of these structures and cannot be accepted.

The simplest type of clasper is that common to the genera *Boloria* (pls. 13 to 29) and *Proclossiana* (pl. 12, fig. 43). The clasper terminates in a concave, distal margin, running up to a dorsal prong which is connected with a second dorsal prong. Proximad of the latter, the harpe unites with the clasper; the head of the harpe, which extends external to the two prongs of the clasper, is a more or less simple process; it bears a row, or rows, of very fine spines on the dorsal margin. The basal branches of the harpe are replaced by a slight concavity, below which the ventral edge extends a little. An unobstructed view of this simple basal end of the harpe is seen in pl. 19, figs. 82, 83, and 84, and pl. 20, fig. 89, etc. In this type, therefore, there is no true internal section of the harpe, the basal half being on a plane with the main body of the clasper. One may add that the two distal prongs of the clasper body are not, as they appear to be in all the photographs, made of denser substance, but are exactly of the same composition as the rest of the clasper. The dark appearance is only caused by the head of the harpe, which is underneath the dorsal edge of the clasper body, the dark edge indicating exactly the ventral line of the head. The latter is completely free from the clasper, the union of the harpe and clasper being, as previously noted, confined to the central area of the harpe, proximad of the basal prong of the clasper.

The next type, though still fairly simple, is decidedly less so than the last; it is found in the large genus *Clossiana* (pls. 10 and 11, and 12, fig. 41). In this type the clasper body terminates in a single sharp tooth, with or without additional smaller teeth surrounding the larger one, or sometimes on it; there is no second prong, nor any distinctive formation of the dorsal margin. There is a moderately strong curvature at the extremity of the clasper, which causes the terminal tooth to be directed more or less inward, rather than dorsally. On account of this curvature it also remains very uncertain what position the terminal tooth will assume in the mount, under the pressure of the cover glass: hence it may appear to be produced dorsally as in pl. 11, figs. 37 and 40, or ventrad as in pl. 10, fig. 31, or even completely lost as in pl. 11, fig. 35. The head of the harpe is bluntly rounded, and bears a number of extremely fine spines. It varies in length considerably, but is otherwise featureless.

We now come to the genus *Brenthis*, the first of the specialised types (pl. 8, and pl. 9, fig. 28). The clasper terminates in an extended distal peak, thickly clothed with long hairs. In the central area of the clasper there is a thickening of the inner chitinous wall, which gives rise to a somewhat triangular-shaped projection, directed dorsally. Nearer the base a second projection rises from the dorsal edge of the external wall of the clasper. These two extensions of the internal and external chitinous walls of the clasper occur in one form or another in all remaining types, and I shall refer to them as the "median" and "basal" prongs, respectively. They must not be confused with the two terminal prongs existing on the claspers of *Boloria* and *Proclossiana* species, which have been described already. Both the latter prongs are located distad of the point of union of the harpe and clasper; they are purely developments of the terminal process of the clasper. In the present case, both prongs are located proximad of the point of union of the harpe and clasper, and are essentially developments of the basal area of the claspers. The ridge from which the basal prong springs (*i.e.* the dorsal rim of the external wall) connects with the phallobase. This is clearly shown in pl. 8, fig. 25, where the ridge lines from the innermost prong of each clasper are seen running to the base of the phallobasic wings. From the base of the median prong (the sharp, triangular peak about the centre of the clasper) the edges of the inner chitinous wall can be seen, one running down to the junction with the vinculum near the saccus, the other extending up to the junction of the vinculum and 9th tergum. These slightly thickened rims mark the boundary of the purely membranous basal area of the inner wall of the clasper. This non-chitinised area varies in extent in different species, but is always present in some degree. The edges of the thickened rims of the inner wall are more clearly seen in fig. 28 (pl. 9), in the left-hand clasper as one looks at the photograph; they are also conspicuous in some figures of species in other genera, as pl. 11, figs. 35 and 37; pl. 12, figs. 41 and 43; pl. 13, figs. 47, 48 and 49, etc. The median prong, if present, is invariably located just distad of the extreme limit of the membranous area.

The harpe carries an internal line of strong teeth, which run from the free head to the base of the ventral branch, the teeth, throughout, being directed distad. The rest of the head is studded with short, but fairly strong teeth. The head is broad over its horizontal plane, and of no great vertical depth. It consequently assumes a variety of appearances in mounted specimens, according to the direction and extent of the pressure. In pl. 8, fig. 24 the extent to which it is free from the harpe can be seen; it will also be noted that the proximal end of the harpe is free from the clasper; the extent to which the separation is carried varies in different species.

The next type (pl. 5, and pl. 7, fig. 21), though bearing some slight similarity to the last, is in reality developed on very different lines; it is found in the genus *Fabriciana*, which includes many species both European and Asiatic. The distal, terminal peak of the clasper is the feature which gives the suggested likeness to the *Brenthis* type; but here the similarity ends. The central thickening in the internal chitinous wall, which culminates in the development of the median prong, reasserts itself ventrally, where at the extreme edge of the clasper, a curious, more or less triangular, free chitinised flap is developed, projecting inwards; no homologue exists in any other Argynnid genus that I have so far examined. The median prong is bluntly rounded off, and is unusually remote from the proximal edge of the sheet. The basal prong is slender, and thickly covered with short spines. In pl. 5, fig. 14, the tip of the basal prongs on each clasper appear to be extensions of the ventral branch of the harpe, which is of considerable length. They are, however, not one continuous piece. Though both processes are of slightly different formation in pl. 5, fig. 13, this gives a more accurate impression of their relative positions. The branch of the harpe passes inside the basal prong; as seen in the photographs it is covering the latter. The head of the harpe is cylindrical, rather snake-like, and covered with short but strong spikes, directed distad. It is free from the clasper for a distance equal to half the entire length of the harpe; this, together with its more or less cylindrical shape, makes it very liable to distortion in mounting. In some species the spikes do not spread completely round the head (pl. 7, fig. 21). The extent of the union with the clasper is unusually restricted; the dorsal branch of the harpe is abnormally inflated; the edge of the ventral branch serrated. Altogether the elaboration of the periphallic organs equals that which we have already seen to characterise the other parts of the genitalia in this genus.

There remain five further highly specialised types, each of which is only represented in Europe by a single species. It is immaterial in which order one takes them, so I continue with pl. 7, fig. 23, *Mesoacidalia charlotta* (= *aglaja* (L.)). Here (also in *Pandoriana pandora*, pl. 2, fig. 4) the harpe and clasper are, in contradistinction to the *Fabriciana* type, more extensively united than in any other type. In fig. 23, the terminal, dorsal ridge of the clasper is seen to be of very irregular formation; the contour of this ridge seems to vary considerably in dfferent specimens. It will be noted that the dorsal margin is darker in the phoitograph; this shade is produced, first by the ventral edge of the head of the harpe which lies underneath, and secondly by an extension of the thickening of the inner wall of the clasper, from the area of the median prong. This extension spreads over the inner surface of the head of the harpe, but does not unite with it; the ridge which constitutes the dorsal edge of the clasper remains free. Only the distal half of the head of the harpe is completely free from the clasper; at the proximal end the harpe and clasper body merge in one, just below the free dorsal edge of the latter. The median prong is unusually large, the peak passing beyond the ridge of the harpe. This peak is not, as it appears in fig. 23, a sharp point; the extremity is circular and flat, and is suggestive of a stick which has been cut off. There is no basal prong. The connection between the head and basal areas of the harpe is extremely narrow; the internal rim of this connecting portion unites with the ventral basal branch. The latter is studded with strong teeth, directed distad; similar teeth run along the dorsal ridge and spread down the flattened sides of the head.

A second of the highly specialised types is shown on pl. 4, fig. 10. The extraordinarily elongated head of the harpe, and its array of dorsal spines, strike the eye at once. Near the extreme distal end a few spines appear on the sides of the head as well as on the ridge. The ventral branch of the harpe is both heavy and densely covered with small but strong spines, which run up to join the dorsal row. The dorsal branch is featureless; the dark appearance in the photograph is caused by this part of the harpe being underneath the gnathus, the dark ventral line of which produces what looks like a long narrow and pointed cleft between the branches of the harpe. This cleft, in reality, does not exist, the two branches of the harpe being united, except at the base. A dark semicircular line, just visible in the photograph between the upturned basal hook of the dorsal prong and the base of the ventral prong, marks the total extent to which the two prongs are divided. The termination of the clasper, suggestive in shape of a fish's tail, is as remarkable as that of the harpe; the dorsal peak of the " tail " is further elaborated by being bifid, a feature which appears in a still more pronounced form in *Argynnis* (pl. 1, fig. 1). The very prominent median prong is of the same nature as that in *Mesoacidalia*, but more developed. The dorsal point is not the sharp point it looks in the photograph, but oval, and the summit flat. It is, unfortunately, impossible to show the real appearance of these prongs in a photograph, unless sections of them could be made; the extreme form of their development is found in *Pandoriana pandora* (pl. 2, fig. 4), where the greater dimensions enable a slightly better idea of the formation to be obtained from the photograph. In this case the median prong rises from the dorsal ridge, and it can be seen to be rounded, and the summit flat. In the two former cases (pl. 4, fig. 10 and pl. 7, fig. 23) only the actual summit of the prong is round, or oval, as the case may be.

The next type is illustrated by *Pandoriana pandora* (pl. 2, fig. 4). The median prong has just been described; there is no basal one. The termination of the clasper is a compound process, a fan-shaped projection densely clothed with hairs, which unites with the harpe and merges, ventrally, with the clasper body. It might be thought that this fan-shaped projection actually constituted a part of the harpe, especially as at its proximal end it appears to originate on the latter; but it is " on," and not from, and as a whole it is, unquestionably, a development of the clasper, with which at its distal extremity it is one; the whole process in fact constitutes a duplication of the dorso-distal area of the clasper. As mentioned before, the harpe and clasper in this species, as in *Mesoacidalia charlotta* (= *aglaja* (L.)), are united to a degree otherwise unknown; only the style, antistyle and distal rim of the area that represents the head of the harpe actually are free. The most striking feature of the harpe is, of course, the development of a perfectly formed style, of great length, which bears an armament of very short, strong teeth. The style is accompanied by a well-developed antistyle, as so often is the case in the Hesperiidi; but there is no structure homologous to the stylifer of the latter, as described by Chapman (1911), the style rising from the dorsal ridge of the head and not from its internal surface. The internal surface of both the style and antistyle in this case is continuous with, and not superimposed on, the internal surface of the rest of the harpe. The area where the stylifer would lie (if present), together with the antistyle and base of the harpe, actually constitute, in this case, the head of the harpe. The presence of the terminal fan-like process of the clasper may account for the non-development of a stylifer, for the fan-like process originates in some degree from the area where the stylifer would normally lie. I have, so far, not come on any other species in which the least suggestion of a style, or antistyle, is to be found; indeed they are the last developments one would have expected to find, judging by the form of the harpe in all other European (and many non-European) Argynnids. The dorsal branch of the harpe is very distended, in proportion to the size of the rest of that structure, and is quite featureless; the ventral branch is long and narrow, and carries several rows of small spines.

In the genus *Argynnis* one finds the last type in which a flat-topped, circular, median prong exists (pl. 1, fig. 1). Here, however, the prong is very narrow; as in *Pandoriana*, there is no basal prong, and the dorsal termination of the clasper is a compound process. At first sight, the latter structure somewhat recalls the end of the clasper in *Issoria lathonia*; but it is not, as in that species, the actual termination of the clasper, but only the dorsal eminence of it. This takes the form of a double-pointed peak, the two points of which lie on the same plane but are directed in opposite directions. The distal point is the larger, and carries a great tuft of long hairs; the proximal one is bifid, similar to the dorsal point of the clasper in *I. lathonia* (pl. 4, fig. 10) but directed proximad and not upwards as in the latter. There is some slight thickening in the chitinisation of the inner wall along the dorsal edge of the clasper body, running as far as the base of the proximal point; this suggests that the terminal double prong may be a compound of a more normal terminal distal peak (as seen in many species) and a displacement of the median prong. This idea is supported by the reduced size of the existing median prong, the orientation of the bifid proximal point, and the fact that no other case, in which the points of a double-pointed process are extended in diametrically opposite directions, has come to my knowledge. We have seen in *Fabriciana* that a small triangular ventral excrescence is developed as an offshoot of the central thickening of the inner wall; it is also a possibility that in the present case the proximal point of the double terminal process has originated in a like manner, only at the dorsal and not the ventral extremity of the affected area. One cannot say which of these two ideas is most likely to be the correct one, but there can be little doubt that this abnormal terminal process is a compound development of some kind, and not a modification of the simple distal peak of the clasper, such as exists in so many species. The harpe is only free from the body of the clasper to a point just preceding the head; the latter is short, broad and rounded, more or less curved, with short but regular, strong teeth. The dorsal branch of the harpe is featureless, the ventral one very similar to the head in size, shape and armament.

There remains one further type, perhaps the most specialised of all, represented in Europe by *Argyronome laodice* (pl. 3, fig. 8). The clasper is without any median prong, but terminates with a rounded protrusion, raised on the inner surface, and studded with coarse short teeth. In fig. 8, only the face of the protrusion is seen, for it rises practically at right angles to the inner surface of the clasper. An homologous structure is found in the clasper of *Erebia atramentaria*, a strange fact that serves to emphasise the degree of specialisation which separates *A. laodice* from other Argynnid species. This process doubtless serves to some extent the same purpose as the inward-projecting terminal point of the clasper in *Clossiana*, though it bears no resemblance to the latter; it is worth noting, however, that in *Clossiana* and also *Argyronome* there is no trace of the development of any median prong on the clasper. The basal prong is represented in *A. laodice* by a triangular excrescence, bearing coarse and fine teeth. The harpe is most elaborate. The dorsal and ventral branches spring practically from the head; the latter occupies more than half the total area of the harpe, and bears a variable number of great teeth on its dorsal edge, interspersed with shorter ones. In contradistinction to this immense development of the head, the basal branches are much reduced in size. About three-quarters of the length of the head is free from the body of the clasper.

This brings us to the end of the European species; many of the remarkable structural features described are, of course, not confined to the European species alone; other equally remarkable ones doubtless remain to be found among the Asiatic and American species.

Before passing to the concise definition of the European genera, I must refer to the subject of individual structural variability, for this is often pronounced. The impression that this variability seems to have made on Reuss is summed up in a single paragraph at the end of one of his papers. He wrote (1921b : 191): " Zu manchen Zeiten und an manchen Orten können verschiedene Arten Individuen hervorbringen, welche einander (von Art zu Art) in den morphologischen Details vollkommen gleichen; entweder reproduziert eine Art die andere oder zwei verschiedene Arten reproduzieren ein gleiches urtümliches Stadium, oft mit fortschrittlichen Merkmalen gemischt. Diese morphologische Variation war den mir vorliegenden Tieren äusserlich nicht anzusehen."

I must admit at once that I find it impossible to agree with this conclusion of Reuss; neither have I come on any case, such as he mentions, of complete identity of structural character among distinct species. On studying many of the details by which he was largely influenced, it seems to me most probable that it was inaccuracies in identification, or some confusion between his dissections, that led him to these mistaken ideas. Thus, in the discussion leading up to the paragraph I have quoted, he states that his genitalia dissections of "*aphirape triclaris*" from North America gave one preparation of a normal *Proclossiana eunomia* (= *aphirape* (Hb.)) and two that were close to *Clossiana selene*; one of the latter was stated to be practically identical with *C. selene.* He gave drawings, of very small size, of these examples (*loc. cit.*, pl. 1, figs. 13 and 14). Some years later (1927) he published a correction of the names of these specimens, stating that the *selene*-like examples were really "*freya*," and that he concluded the bodies on his specimens must have been changed. He had also discovered that Petersen (1904) had figured the genitalia of "*freya*" as "*chariclea*," and this had misled him. At a still later date, Reuss informed me *in litt.* that his fig. 13 was "*freija*," and fig. 14 "*selene*." This shows that some further confusion must have existed in connection with his mounts of these specimens. I have mentioned already that Reuss regarded much of the structural elaboration found in the Argynnids as purely superfluous, and the outcome of uncontrolled variation. I cannot help thinking that this idea also was partly due to confusion arising from insufficient attention to detail. He especially emphasises the case (1922c) of an aberrant example of the uncus of *Argynnis paphia*; he illustrated this with a very small drawing (1922c : 366, fig. 2). This figure was accompanied by others, one of which (fig. 7) was marked "*ruslana*," but this, he has informed me (*in litt.*), was a mistake, and should read "*zenobia*." The repetition of such slips cannot but leave an element of doubt, especially in the case of abnormal specimens. The specimen of *A. paphia* (Reuss's fig. 2) showed an uncus of equal depth over all its length, and a terminal point such as occurs in *Mesoacidalia charlotta* (= *aglaja* (L.)). It has no dorsal crest, but bears a few short, even spines. Reuss concludes this uncus to be the result of a mutation producing the type of uncus found in *Damora sagana*; and further, as in the case of *Clossiana selene* just mentioned, that it was an example of how any species is liable, through mutation, to assume the structural characters of any other related species. He also claimed that such mutation produces wholly superfluous and valueless structural elaboration, asserting that many of the elaborate processes found in the Argynnids (especially those of the claspers) are of such a nature. I have already shown that these claims are largely based on false premises, and that in fact, so far as I can ascertain, there is no known case of the genitalia of one species being produced in another. I can find no valid reason for assuming the abnormal uncus of *Argynnis paphia* to be a *Damora* mutation appearing in *Argynnis*. Judging from Reuss's figure, described above, the only characters exhibited by the uncus that are common to it and the uncus of *Damora*, are the even depth, and the terminal point. Both these characters, however, might apply equally to *Mesoacidalia charlotta* (= *aglaja* (L.)). According to Reuss (*loc. cit.*) the *Damora* uncus has a unique dorsal elaboration, proximad of such ridge-spines as it develops; this is certainly its most characteristic feature. Of this peculiar structure there is not the least sign in his abnormal *A. paphia* uncus; without it, no claim that this uncus is a *Damora* mutation arising in another species can be upheld. On the other hand, the features are such that they might be produced by simple malformation of the normal *A. paphia* uncus. The dorsal crest is known to vary greatly in development; in *Fabriciana*, though usually well developed, it is wanting in at least one species, and possibly others. Its loss in an aberrant specimen of *Argynnis paphia* would be nothing very remarkable, and the crest excrescences remain, which is what one would expect in such a case; they are known to do so in similar circumstances in *Fabriciana*. The terminal point, springing from the dorsal ridge and not produced from both the dorsal and ventral edges, is, seemingly, a character abnormal to the species; but the whole organ is stunted, and the full depth retained to the extremity, where the normal curved tip has not been developed. In these circumstances, one of the dorsal spines, which are located between the crest and the tip (as shown in pl. 1, fig. 3), might easily be produced into a terminal point such as is shown in Reuss's drawing. It is unfortunate that in that drawing Reuss gives no indication of the point where the union of the ventral edges of the uncus is situated, and this, of course, makes it very difficult to form an accurate idea of the development of the organ. The impression I gather is that the drawing is incomplete, especially in the basal section, and, as so often happens with such camera sketches, was made to illustrate some one, or perhaps two features; in this case, apparently, the absence of the crest, more than anything else. In consequence, it fails to show details that were probably omitted just because they were not striking, but which, all the same, are necessary to the understanding of the parts that are shown. It is one of those cases that demonstrate the far greater value of even a bad photograph, which shows the entire organ, than a drawing showing only an outline of the striking features and leaving the very essential background to the imagination. If the basal portion of the uncus, from its junction with the 9th sternum, had been included in detail by Reuss in his drawing, and if the missing portion were more or less normal (as Reuss tells us the associated structures were), it would be found that the entire segment differed much less than might be supposed from a typical example. I cannot, therefore, accept this specimen as anything but a malformed one; such malformations are by no means rare in the Argynnids. Natural variability, which is present in the vast majority of specimens (and of which numerous examples are shown on the plates), does not destroy the characteristics of the species, or produce others which are not normally present.

There is more to be said for the possibility of the second of Reuss's suggestions, namely, that the specimen was an example of reversion to a simpler type from which both *Argynnis paphia* and *Damora sagana* may have been evolved. The perfect development, however, of the other specialised structures of typical *Argynnis* form, opposes this theory; for the degree of constitutional isolation in which we have seen the various Argynnid genera now stand indicates that the period of common ancestry must be so remote that reversion to the type of structure then prevailing would be scarcely probable, if indeed it were possible. The characters of those periods must long since have given place to the intermediate ones, the forerunners of the present specialised types; and such intermediate characters may still be latent in the nature of the species. It is obvious, however, that such characters could have nothing in common with the present-day types of other genera, each genus having been evolved on divergent lines, as is witnessed by the existing group-specialisation.

Finally, one should note that there are many instances of highly specialised forms of one organ being correlated with equally specialised forms in others. The lyre-like wings of the phallobase and the narrow, cylindrical, harpe head in *Fabriciana* provide one very marked example. Such correlated specialisation is a further proof of the complete segregation of the lines of evolution, which have led up to the isolated positions of most of the existing genera.

III. The Generic Divisions of the Argynnidi, with Definitions of the European Genera.

The subdivision of the Argynnidi is a subject that has not attracted much attention. A few writers have endeavoured to deal with the species in smaller groups, or genera, but have mostly failed to define them very clearly. Of the names that have been used in various publications, *Issoria* Hübner, *Dryas* Hübner and *Brenthis* Hübner have been most often selected, especially in this country. *Issoria* was accurately applied; *Dryas* and *Brenthis* inaccurately. The last has been used in widely differing senses by different authors; some apparently made the definition of the genus merely a question of the size of the species, others accepted (in theory) Felder's definition which was based on the position of nervure 10 on the fore-wing. The latter definition places the genotype, as well as the only other true species of *Brenthis*, all in *Argynnis*. Most authors, however, have ignored the definition, and placed the true Brenthids in the genus, along with a varying number of other species which had no claim to such a position, but which came in under Felder's definition. If any further comment on the value of this definition were needed, it is supplied by the fact that, if strictly applied, individuals of some species would be in the awkward position of belonging to two different genera, because the neuration of the left wing might be *Argynnis* and the right *Brenthis*, or vice versa. Faced with such an absurdity, it is not to be wondered at that some authors maintained that division of the Argynnidi was unnecessary, if not impossible. This was the position when Reuss began to publish his data on Argynnid classification. Changes such as he advocated, however, are never popular. It is strange how many collectors will accept without question any system of classification, so long as it is alleged to be based on characters they can easily see, displaying complete indifference to the fact that it may be entirely erroneous from the point of view of natural relationship.

The position actually is, that as soon as a systematist turns his attention to any group of the Argynnidi, he finds comparative description within the traditional " genera " impossible, owing to the mixture of species included in these purely artificial groups. These indefinable divisions are, of course, worse than useless; those who are willing to accept them forget that the more closely their work accords with them, the more certain is it that they are perpetuating inaccuracies and adding fresh misconceptions to complicate matters in the future. It is now twenty-two years since Reuss's anatomical researches first disclosed the fact that the uniform coloration and pattern of the upperside of the numerous species of Argynnids is a tribal character, and not a generic one; and that the genus *Argynnis* (s.s.) is but one of many genera included in this great tribe. Although there may be some who are reluctant to accept this view, I know that systematic workers in Europe and America have done so, and I trust it may not be too much to hope that the plates accompanying this work will help entomologists (in this country at any rate) to realise how little in common there is between the majority of the highly specialised genera that together constitute the tribe Argynnidi.

In giving definitions of the European genera I have followed Reuss's work so far as possible; that a few alterations have been necessary, is not surprising. Many groups that Reuss at first established as subgenera, he later converted into genera; an action that was fully justified. Others of his subgenera I have not found sufficiently characterised to uphold. Some mistake seems to have occurred in the selection of his type for the genus *Prodryas* (later changed to *Protodryas*), which has invalidated both these names. It was necessary to bring in one new genus. In order to give as full an idea as possible of Reuss's work, I have included the non-European genera he dealt with, but without defining them. It seems probable that the number of these will have to be increased in the future, though, of course, very many non-European species come within the European genera. As to the order in which I have taken the genera, until the Asiatic and American species have been worked over, this can only be provisional; but it is probable that the position of the first five will not require to be altered. *Boloria* and *Proclossiana* are certainly the most generalised, and the next three follow them naturally.

In the following definitions I use the term " simple " as implying the absence of elaboration of form in any given structure, which does not mean the absence of specialised development, or that the structure exhibits the simplest formation of its kind. I may emphasise the fact that, though it would be possible to define these genera on the characters of the uncus alone, or those of any other major process of the 9th or 10th abdominal segments (all of which exhibit generic characters of paramount importance), I employ them all; for though this complicates the actual definitions, it displays an array of facts which demonstrate the individuality of each genus in an irrefutable manner. To shut one's eyes to such facts, is to disregard the true affinities between respective groups of insects, as witnessed by morphology, a course that can scarcely be advocated by anyone; yet it is obvious that to uphold the past conceptions of genera that cannot be defined is tantamount to doing so.

In one or two cases I have had to define genera on the characters of the type species alone. I have, therefore, intentionally made the definitions as broad as possible, in order to avoid the accidental inclusion of characters which might exclude some of the extra-European species that really belong to the genus, but which at present I have not personally examined.

(1) Genus *Boloria* Moore, 1900, *Lepid. Indica* **4** : 243; type *Papilio pales* Schiff.

Uncus simple, short, deep in proportion to length, slightly curved downward, terminating bifid; *gnathus* wanting; *wings of phallobase* simple, short, in shape suggesting the winged seed-pod of some plant, narrow at base, expanding to distal extremity, which is rounded; *aedeagus* simple, short, broad in proportion to length, endophallic tube bearing patches of very fine, chitinous scales; *claspers* simple, with double dorsal prong at distal extremity; *harpe*, distal half free from clasper body, head of varying length, tapering to distal extremity and carrying fine spines on dorsal ridge (pls. 13–29).

Includes *B. pales*, *B. napaea* and *B. graeca ;* all represented by numerous subspecies, especially the first.

(2) Genus *Proclossiana* Reuss, 1921, *Ent. Mitt.* **10** : 190; type *Papilio aphirape* Hb. (= *eunomia* Esp.).

Uncus simple, extremely slender in proportion to length, straight, slanting slightly upwards and raised just above dorsal plane of 9th tergum, terminal point curved downwards and shallowly bifid; *gnathus* wanting; *wings of phallobase* simple, shape suggesting winged seed-pod of a plant, very narrow at base and greatly expanded at distal extremity; *aedeagus* simple, endophallic tube bearing patches of very fine chitinous scales; *claspers* simple, with double dorsal prong at distal extremity; *harpe* with distal half free from clasper body, head simple, equal in depth all over, carrying fine spines on dorsal ridge (pl. 12, figs. 43, 44).

The type is the only representative of the genus, so far as is at present known. Reuss (1936) adds *triclaris* Hb. as a distinct species; his notes on the structural characters of that insect, however, leave some doubt as to whether this claim can be substantiated.

Proclossiana and *Boloria* have closer affinities than any other two of the European genera; all the same the very remarkable form of the uncus, harpe head, and much more marked development of the wings of the phallobase in the former, exclude any possibility of uniting them. It may be noted that the elevation of the uncus above the level of the dorsal plane of the 9th tergum in *Proclossiana* is a peculiarity only known in one other European genus (*Argyronome*). It is further noteworthy, that most writers include *P. eunomia* with the *selene* group of species, *i.e. Clossiana :* the fact of the close relationship between *Proclossiana* and *Boloria* demonstrates the impossibility of uniting the former with *Clossiana*.

(3) Genus *Clossiana* Reuss, 1920, *Ent. Mitt.* **9** : 192, footnote; type *Papilio selene* Schiff.

Uncus strong, short and deep in proportion to the length, sharply curved downward, and terminating deeply bifid; *gnathus* wanting; *wings of phallobase* simple, expanding to greatest breadth centrally (figs. 37 and 41, best illustrations); *aedeagus* elaborate, very broad centrally in proportion to length, proximal end narrow and tubular, dorsal area before central expansion largely unchitinised, distal end reduced to narrow, ventral plate, endophallic tube bearing strong, chitinous teeth, in eversible portion of membrane, and producing latero-distal flaps with strongly chitinised margins; *claspers* with single dorsal prong at distal extremity, directed inwards; *harpe* free at head, which terminates bluntly rounded, and bears very fine marginal spines (pls. 10, 11, and 12, figs. 41, 42).

Includes the European species *C. selene*, *C. selenis*, *C. euphrosyne*, *C. dia*, *C. thore*, *C. titania* (= *amathusia* Esp.), *C. freija*, *C. frigga*, *C. polaris*, *C. chari-*

clea, *C. improba*, and a large number of Holarctic species, estimated by Reuss (1921) at 21.

(4) Genus *Brenthis* Hübner, [1818], *Verz. bekannt. Schmett.* (2) : 30; type *Papilio hecate* Schiff.

Uncus highly specialised, short, broad, very slightly curved downwards, terminating trifid; *gnathus* wanting; *wings of phallobase* simple, attaining greatest width just above the base, tapering markedly to extremity (best illustration fig. 28); *aedeagus* broad at proximal end, only slightly increased in width centrally, reduced distally to narrow, ventral plate; phallobasic tube developing latero-distal flaps, the margins of which are very slightly chitinised; *claspers* terminating in pointed dorso-distal extension; *harpe* free at head, which is clubbed, slightly flattened, and studded with teeth (pls. 8 and 9).

Includes *B. hecate*, *B. ino*, *B. daphne*.

(5) Genus *Issoria* Hübner, [1818], *Verz. bekannt. Schmett.* (2) : 31; type *Papilio lathonia* L.

Uncus simple, short, very slightly curved downwards, terminating in a blunt point, bearing a few minute teeth (three of these can be made out in fig. 11); *gnathus* very elaborate, complete ventrally, with extensive lateral development, studded externally with very short teeth; *wings of phallobase* long, broad at base and tapering to extremities, which are more or less pointed; *aedeagus* simple, long, broad at base and tapering continuously to pointed, distal extremity, endophallic tube bearing a small central patch of spines of varying sizes; claspers terminating in a dorsal bifid tooth and a ventral point, together suggestive in form of a fish's tail; harpe free for two-thirds (or more) of length, head elongated, flattened, more or less uniform in depth, terminating rounded, bearing a row of strong teeth on dorsal ridge (pl. 4).

Synonyms :—*Rathora* Moore, 1884, *Lep. Indica*, type *Papilio lathonia* L.; *Kükenthaliella* Reuss, 1922, *Arch. Naturgesch.* **87** (A) 11 : 223; type *gemmata* (Butl.).

Though I have not myself examined any of the extra-European species, judging from Reuss's notes on the genitalia of *I. gemmata* (1922a) it appears that this species is an *Issoria*. Reuss had formerly used *Rathora* in place of *Issoria*, but he later corrected this (1936) and in his note seems to have included the *gemmata* and *excelsior* groups under *Issoria*. The genus therefore includes *I. lathonia* in Europe, and a number of Asiatic and African species as well.

(6) Genus *Fabriciana* Reuss, 1920, *Ent. Mitt.* **9**: 192; type *Papilio niobe* L.[1]

Uncus specialised, deeply curved ventrally, proximal half broad and deep, greatest depth attained at about half the length, tapering over distal half and terminating in a sharp

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[1] It is as well to note here that "*Papilio niobe* L." selected by Reuss as type of *Fabriciana* is not the insect usually associated with the name. Actually the "*niobe*" of Linnaeus was the insect known as "*eris*" Meig.; while *cydippe* Linnaeus and its synonym *adippe* both denote the insect now known as "*niobe*." From the point of view of nomenclature the position of these names is extremely complicated, but Mr. F. Hemming is preparing a detailed account of the facts which will enable the real names of these species to be established. At the moment the names "*adippe*" and "*niobe*" have had to be employed in this work in their present artificial sense, as it is best to await the publication of the full details before making changes. Mr. Hemming has recently dealt with the case of *Papilio aglaja* L. (Hemming, 1942, *Proc. R. ent. Soc. Lond.* (B) **11**: 155–160) and shown that the valid name for the species is *M. charlotta* (Haw.); this name has accordingly been adopted in this work.

point, bent abruptly down at almost a right angle; dorsal ridge jagged over a restricted area, the jagged edge raised on a vertical crest in many species; *gnathus* represented by two overlapping, chitinous plates, attached to the 9th segment at the point of union of the tergum and vinculum; *wings of phallobase* extremely specialised, lyre-shaped, each wing bearing a fin-like projection centrally, and terminating in a sharp point (in shape like the beak of a bird); *aedeagus* simple, broad at base, uniform in width throughout, endophallic tube bearing central patch of strong, chitinous teeth and scales; *claspers* complex, terminating in extended dorso-distal point bearing a thick brush of long hairs, and developing an internal flap-like ventral extension of the inner chitinous sheet; *harpe*, free for approximately half its total length, head cylindrical, studded with short, coarse spikes (pl. 5, figs. 13, 14; pl. 6, figs. 15–18, and pl. 7, fig. 21).

Synonyms :—*Prodryas* Reuss, 1927, *Dtsch. ent. Z.* **1926** : 434; type *kamala* (Moore). As this generic name was preoccupied, Reuss replaced it by *Protodryas* Reuss (1928, *Int. ent. Z.* **22** : 146, same type).

Both these genera fall to *Fabriciana* as their type, *kamala* Moore, is a typical *Fabriciana* in every respect. There seems to be little doubt that, in citing *kamala* as type of *Prodryas*, Reuss was misled by the form of the uncus, which, as I have previously noted, has no dorsal crest. He describes it (1922a) as being similar to the uncus in " *Rathora*," i.e. *Issoria*, which of course is quite a mistake, the whole form of the uncus being typical of *Fabriciana*, i.e., the dorsal and ventral outline, depth, curvature, dorsal serration, terminal right-angled point, and ventral angle; none of these features occurs in *Issoria*.

Subgenus *Profabriciana* Reuss, 1926, *Dtsch. ent. Z.* **1926** : 70; type (and only representative) *jainadeva* (Moore).

To this subgenus Reuss adds (1927) *elisa* Godt. and *auresiana* Frhst. (Reuss considers the latter to be an African form of the former). I have not dissected *jainadeva*, so cannot be certain as to the validity of *Profabriciana*; but assuming Reuss correct in bringing *elisa* into this subgenus, this would automatically sink *Profabriciana* as a synonym of *Fabriciana*, for *elisa* cannot be placed in a separate genus from *niobe*.

The genus *Fabriciana* therefore includes : *F. niobe*, *F. elisa*, *F. adippe* and *F. taigetana* Reuss, in Europe; *F. kamala*, *F. jainadeva*, and many other non-European species. *F. taigetana* is included, as a species, on the strength of Reuss's description : I have not been able to examine or dissect a specimen.

The separation of the genus *Fabriciana* demonstrates two very interesting points in connection with the pattern of the underside in Argynnid species. First : the resemblance that has led so many writers to assume that *F. elisa* was closely related to *Mesoacidalia charlotta* (= *aglaja* (L.)); and second, that *F. kamala* is usually placed in close association with *Argynnis paphia* in text books, for similar reasons. If, however, one examines the silver markings on the underside of *F. kamala* carefully, it will be seen that they are not really stripes, such as exist in *A. paphia*, but are composed of enlarged spots, developed so as to touch the nervures fully on each side, but still separated by the latter, while the row at the outer margin of the wing are crescent-shaped, not uniformly flat, internally, as in *A. paphia*. These silver markings, in fact, are those of the *niobe*-type, modified slightly, but sufficiently to obscure the true affinities of the species.

In *F. elisa*, also, modification of the characteristic markings of the underside has been misleading, hence the false likeness to *Mesoacidalia charlotta* (= *aglaja* (L.)). One must note, however, that Lang (1884) pointed out that *F. elisa* " is in fact much more nearly allied to *adippe* or *niobe* than *aglaia*, as may be seen by the presence of the round, silver-punctured spots between the marginal and central rows." This observation has been largely ignored by more recent writers, but testifies to the accuracy of Lang's work.

(7) Genus *Neoacidalia* Reuss, 1926, *Dtsch. ent. Z.* **1926** : 69; type *Papilio cybele* Cr.

Includes no European species, but, according to Reuss (1926), four Asiatic and thirty-four American species.

(8) Genus *Mesoacidalia* Reuss, 1926, *D. ent. Z.* **1926**, Heft 1 : 69; type *Papilio aglaja* L. (= *charlotta* Haworth).

Uncus specialised, curved downwards, deep, of nearly equal depth throughout, dorsal ridge produced to form terminal hook, and a very slightly developed dorsal crest, which is jagged over its whole length; *gnathus* represented by two overlapping, chitinous, ventral plates (similar to those existing in *Fabriciana*, and the only formation common to both genera); *wings of phallobase* simple, small in proportion to size of periphallic structures, broad at base, nearly uniform in width throughout, rounded at extremities; *aedeagus* blunt and broad, endophallic tube bearing dense central patch of strong, though small, chitinous teeth, the eversible portion being thickly covered with very fine chitinous scales; *claspers* terminating bluntly rounded, dorso-distal margin irregular, developing an insignificant blunt point; *harpe* united with clasper body except at the distal end of the head, which is deep and flattened, bearing dorsal and lateral rows of sharp, strong teeth (pl. 6, figs. 19, 20; pl. 7, figs. 22, 23).

Includes *M. charlotta* (= *aglaja* (L.)), *M. alexandra*, *M. lyauteyi*, and possibly further species such as *M. clara* Blanch., which Reuss (1926) places in the separate subgenus *Proacidalia* Reuss (1926, *Dtsch. ent. Z.* **1926** : 69).

(9) Genus *Argynnis* Fabricius, 1807, *Mag. f. Insektenk.* (Illiger) **6** : 283; type *Papilio paphia* L.

Uncus elaborate, long and slender, bent abruptly downwards close to base, tapering to sharp, terminal, curved point, a fin-like crest of varying vertical expansion, rising from dorsal ridge over proximal area, and bearing variable number of long, narrow teeth, directed distad; *gnathus* represented by two overlapping ventral plates, located at lateral bases of 9th tergum; *wings of phallobase* short, expanding continuously, distal extremity flat; *aedeagus* highly specialised, broad at base, where the circumference of the aedeagal wall is complete, elsewhere incomplete and replaced by dense spinal armament of endophallic tube, which stretches almost the entire length of the aedeagus; *claspers* terminating in compound dorso-distal prong; *harpe*, head free, short in proportion to total length, broad and terminating bluntly rounded off, studded with very coarse short teeth (pl. 1).

Synonym :—*Mesodryas* Reuss, 1927, *Dtsch. ent. Z.* **1926** : 435; type *Papilio paphia* L.

A. paphia is the only European representative of the genus.

It may be interesting to recall the difficulty that arose following Reuss's selection (1928) of *Papilio niphe* L. as type of the genus *Argyreus*, owing to the want of any precise form of classification in the tribe. As both *niphe* and *paphia* were then included in the inclusive genus *Argynnis*, the latter became a synonym of *Argyreus*; following on this it became necessary to get the International Commission to suspend the rules, in order to retain the generic name *Argynnis*, which had been continuously employed since 1807. This action, as we now see, would not have been required if a system of classification taking cognizance of the natural relationship of the insects had been in use.

(10) Genus *Pandoriana* Warren, 1942, *Entomologist* **75** : 246; type *Papilio maja* Cr. (= *pandora* [Denis & Schiffermüller]).

Uncus elaborate, deep, slightly curved, terminating in sharp, simple tooth, a fin-like crest of considerable expansion rising from dorsal ridge over total length, and bearing variable number of short, broad teeth, directed distad; *gnathus* represented by rudiments of two ventral plates, located at lateral bases of 9th tergum; *wings of phallobase* simple in outline, uniform in width, with slight expansion at distal extremity, which is rounded; *aedeagus* slender in proportion to length, of uniform width, endophallic tube bearing extensive patch of coarse spines, which replace the aedeagal wall before the distal extremity, and a sprinkling of fine, chitinous scales on eversible portion of tube; *claspers* complex, termination rounded and clothed with long hairs, dorso-distal ridge partially duplicated; *harpe* highly specialised, extensively united with clasper body, head replaced by a long style studded with short teeth and a broad short antistyle (pl. 2).

Type the only European species.

Reuss (1926) placed the species in *Protodryas* (type *kamala*), together with *anadyomene* Fldr. *Protodryas* has been shown to be a synonym of *Fabriciana*. I have not dissected a specimen of *anadyomene*, so am unable to place it in any genus with certainty; it seems likely it is a *Pandoriana*, but there is the possibility that it is an *Argynnis*.

(11) Genus *Childrena* Hemming, 1943, *Proc. R. ent. Soc. Lond.* (B.) **12** : 30; n. n. pro *Eudryas* Reuss. Type *Argynnis childreni* Gray.

Synonym :—*Eudryas* Reuss, 1926, *Int. ent. Z.* **20** : 253; a homonym of (a) *Eudryas* Boisd., 1836, Roret's *Suit à Buffon* (*Lép.*) **1** : explic. pl. 14; (b) *Eudryas* Harris, 1841, *Ins. Massachusetts* : 310; (c) *Eudryas* Fitzinger, 1843, *Syst. Rept.* **26**; (d) *Eudryas* Gistl, 1848, *Nat. Thierr.* : viii.

No European species.

(12) Genus *Argyreus* Scopoli, 1777, *Intr. Hist. Nat.* : 431; type *Papilio niphe* L.

Synonyms :—*Acidalia* Hübner, [1818], *Verz. bekannt. Schmett.* (2) : 31; type *Papilio niphe* L.; *Mimargyra* Reuss, 1922, *Arch. f. Naturgesch.* **87** (A)11 : 221; type *Papilio hyperbius* L. (= *niphe* L.).

No European species.

(13) Genus *Damora* Nordmann, 1851, *Bull. Soc. Nat. Moscou* **24** (4) : 439; type *Damora paulina* Nordmann (= *Argynnis sagana* Dbl.).

No European species.

(14) Genus *Argyronome* Hübner, [1818], *Verz. bekannt. Schmett.* (2) : 32; type *Papilio laodice* Pall.

Uncus highly specialised, long and slender, tapering over whole length, bent upwards at the point of union (ventral) of the lateral edges, and rising sharply above plane of 9th tergum, terminating in hooked tip, directed downwards; *gnathus* wanting; *wings of phallobase* massive, widely separated at base, expanding greatly to distal extremity, which is folded over on itself; *aedeagus* massive, base bifid, greatly expanded centrally, reduced distally, endophallic tube bearing dense spine mass, replacing aedeagal wall over distal half; *claspers* complex, terminating in rounded, inward extension; *harpe* complex, head very elaborate, practically free from clasper, and bearing numerous strong teeth of variable lengths (pl. 3).

Synonym: *Eudaphne* Reuss, 1922, *Arch. f. Naturgesch.* **87** (A)11:221; type *Papilio laodice* Pall.

The type is the only European species.

IV. Speciation in the Genus *Boloria*.

The genus *Boloria*, as defined in the last part, includes three species. The component races of these constitute what has been known as the "*pales* group." Before dealing with this small genus systematically, we must consider the question of speciation.

The genus *Boloria* is the most generalised genus of the tribe; for this reason the recognition of specific limits among so large a number of races (twenty-seven, or more) is bound to be difficult. Authors differ very considerably in the views they have expressed on the subject, but when one comes to make a careful examination of the varying data on which they base their arguments, it transpires that in most cases they were dealing with but one or two races, and often their knowledge of these was only within a limited area. Thus, many English collectors have asserted with confidence that the race referred to as "*arsilache* Esp." was a species distinct from *pales* Schiff., principally because the former is known to be a bog insect. Yet, in many cases, their knowledge of these races was derived from the Swiss forms only. Many seem to confuse *B. napaea* Hoff. with *B. pales* Schiff., and to have little idea what the finest form of the latter, from the eastern Alps, looks like. On the other hand, very few collectors in central Europe, who are familiar with the eastern, typical *B. pales*, have held the view that "*arsilache* Esp." was a distinct species; their difficulty has been to distinguish these two insects. As so often happens in such cases, the inability to obtain a clear result leads workers to opposite extremes. Some, like Reuss and Higgins, have assumed that the many races must be units of four or five species; others, like Verity, have maintained that all are to be placed in one. My own view, as already mentioned, falls between these two extremes; but it was not until after two years of research, involving the dissection of twenty-four of the known races of *Boloria*, as well as numerous other Argynnid species, that I was able to satisfy myself that all the available facts, morphological, ecological and biological, were in agreement in the classification I finally have adopted.

Verity dealt with the geographical variation of *B. pales* in some detail, and at the same time elaborated his theory that all known races belonged to one species (1932). With certain of his postulates I agree; such as when he states "the only practical proof one can safely accept of real specific distinction between two allied groups is that they should be known to occur together in some localities and that there should exist no transitional individuals anywhere, showing they do not interbreed." Personally I would omit the "only," though otherwise I agree; unfortunately, however, the data he then puts forward are frequently questionable, especially in respect of so-called "transitions"; consequently some of his conclusions appear to be based on false premises. This compels me to deal somewhat fully with the points he raises.

To start with, Verity says, writing of *B. pales* subsp. *pales*, subsp. "*arsil-*

ache," subsp. *generator* and *B. napaea* (1932 : 105) : " According to my standard of species, these are only exerges, with slightly different constitutions, each of which picks out the spots which suit it best and where it has an advantage over the others and it excludes them ; " with which I again agree (if the *B. napaea* be omitted), noting that in such circumstances Verity's " exerges " would constitute what are usually known as " subspecies " : but he continues, " transitions do exist and they are not found together without transitional individuals amongst them, so that they cannot be species." Now I do not know if *B. napaea* and *B. pales* subsp. *generator* ever do occur together; but so far as *B. pales* subsp. *pales* and *B. napaea* subsp. *napaea*, and the latter and *B. pales* subsp. *aquilonaris* (= " *arsilache* " as used in this particular instance by Verity) are concerned, they *do* occur together without transitions; so on Verity's own postulate *B. napaea* would be a distinct species. It is remarkable how few entomologists realise that the typical races of *B. pales* and *B. napaea* continually occur together, and not only this, but that the dates of their emergence often coincide. In my own experience alone, I have come on several striking examples of this. One was on the well-known " Latemar Meadow," under the great cliffs of the Latemar, above the Karer Pass, where both species occurred at the same time in this very restricted and isolated spot, although neither was found in neighbouring localities which seemed very suitable. Again, in the mountains above Mallnitz in Carinthia, on an alp, about 5700 feet altitude, the first male *B. pales* and *B. napaea* appeared on the same day and at the same spot. In Switzerland I have found the two together in many localities in the Grisons, *i.e.* the Val Minor; between Pontresina and Morteratsch; the Roseg Tal, etc.; in western Switzerland, on the Dent du Midi and the Grammont. Both insects vary a good deal everywhere, in size and colour; but there is nothing in such variation that could accurately be described as constituting transitions between the two species. The idea that an individual is a transitional example springs to the mind very readily (as I know from past experience) when one is uncertain as to the exact characteristics of either species, especially when dealing with two species that at all times resemble each other as much as *B. pales* and *B. napaea*. But with familiarity one begins to recognise aberrant specimens for what they really are; and it should be noted that similar variations occur in either species in the absence of the other, which is irrefutable proof that they are not the result of interbreeding. Further, as I will show, such aberrations remain morphologically typical of the parent species, and would appear to be the outcome of parallel mutations in somewhat similar forms and not in the least the development by one species of the characters of the other. Were such development actually taking place, the structural characters would not remain unaffected, for, as I have shown in other families (1926 and 1936), subspecific structural characters are never constant. So far as these two species are concerned, then, Verity's data are obviously inaccurate. Turning to *B. napaea* and *B. pales* subsp. *aquilonaris* (the " *arsilache* " of most writers—but not of Esper—*hypoarsilache* Verity, and the mythical " *lapponica* " [2] Staudinger), we find the same situation. *B. napaea* occurs in many localities with this subspecies of *B. pales* which, as is well known, occurs in swampy localities, often of no great area. Immediately surrounding such areas *B. napaea* often flies, for it too is quite at home in swampy localities; in such places both species often are to be seen flying together. It has frequently been recorded that in Switzerland *B. pales* subsp. *aquilonaris* is restricted to boggy tracts surrounding small lakes, but the presence of *B. napaea* in these localities is ignored, presumably because it does not penetrate quite into the watery parts of the swamps after the manner of the former. *B. napaea*, of course, is found in countless boggy, or partially boggy, localities where *B. pales* subsp. *aquilonaris* does not occur. I have come on it repeatedly in such localities, as, for example, above Lenzerheide in the Grisons, where on a swampy moor-like tract, the home of *Parnassius phoebus*, *Lycaena hippothoë eurybia*, etc., *B. napaea* occurred in the utmost profusion. Many records of such localities exist, but pass unnoticed; it may be of interest to mention a few, from widely separated districts. Goltz (1909) records the species on swampy ground at the east end of the lake Ritom; Tutt (1907a) records " *Brenthis pales* " by the Lac d'Allos " in thousands," and from his notes one gathers that both *B. pales* and *B. napaea* were present. He does not actually mention the nature of the ground, but the fact that he took " *Chrysophanus hippothoë* " at the same time, speaks for itself. (Those who regard both *B. napaea* and *B. pales* as inhabitants of dry ground will be surprised if they note how frequently these species are found flying with *Lycaena hippothoë*.) Tutt again records (1907b) *B. pales* and *B. napaea* flying this time with *Clossiana selene* on " flat marshy " spots in the Goeschenen district; and (1908a) between Airolo and the summit of the St. Gothard Pass " in a small damp and marshy spot," *B. pales* again in company with *L. hippothoë*, and at higher levels " wherever a marshy flat appeared." Yet again, Tutt tells us (1908b) that " a marshy slope " above Preda on the Albula Pass gave him *B. pales* and *L. hippothoë*, and from his remarks it is clear that the two *Boloria* species were present; lastly, on the summit of the Arlberg pass, Tutt records (1910) that on " small, flat, swampy patches " on each side of a small stream, " *Brenthis pales* " was abundant at about 6500 feet; and Cooke (1938), referring to what is apparently the same locality, states that he took both *B. pales* and *B. napaea*. But if the majority of collectors overlook the fact that both these species are absolutely at home on bog and marshland, Dadd (1925) has gone to the other extreme; for he states that *B. napaea* occurs only on swampy ground. This, of course, is not the case. He qualifies his statement, however, by saying that he has not sufficient data to be sure if the species is completely confined to swampy regions in all districts.

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[2] See *B. pales* subsp. *aquilonaris* (p. 72).

As long ago as 1861, Staudinger recorded that on the outer limits of boggy areas in Lapland " *pales* " and specimens transitional between it and " typical *arsilache* " flew together; adding that, owing to these transitional specimens, it was impossible to distinguish between the " *arsilache* " and the " *pales* " (1861). In actual fact, the insects Staudinger seems to have taken for " *pales* " were *B. napaea* and its small arctic form which I am dealing with in the systematic part of this work as f. *frigida*. His " typical *arsilache* " and the " transitional " specimens were, probably, all the subsp. *aquilonaris* of *B. pales*. (Typical specimens of the latter do not occur in Scandinavia, so far as I can ascertain; Dr. L. G. Higgins, who has made a considerable study of the northern forms of *Boloria*, tells me (*in litt.*) that he has never seen a Scandinavian specimen either.) These records of Staudinger's in respect of localities have been corroborated by most collectors who have given us records of collecting in Scandinavia; but unfortunately his other remarks on these insects have been completely misunderstood, and he has been credited with describing a " race " as " Var. *lapponica*," though in fact at that time he had not done so, and actually no such race exists. What he did do was to record that he had not taken this supposed insect in Norway at all. (See details under *B. pales* subsp. *aquilonaris*, p. 72). Most collectors who have been to Scandinavia claim to have found " *arsilache* " and " *pales lapponica*," in swampy and dry localities, respectively;

but invariably the specimens they have taken prove, when examined, to be a mixture of *B. pales aquilonaris* and *B. napaea* f. *frigida*; very frequently both species come from one locality. In many instances it seems that the collector is so blinded by the theory of the " wet " and " dry " segregation of " *pales* " and " *arsilache*," that he names his captures according to the nature of the locality. Staudinger tried to distinguish between the type of marsh, and the degree of wetness, of the localities favoured by " *arsilache* " and " typical *pales*," but concluded that these two are one species, which is correct, though actually he had two species before him at the time of writing.

Thus we see that true *B. napaea* in central Europe and southern Scandinavia and the small arctic form *frigida* in northern Scandinavia fly in certain localities with *B. pales pales*, or subsp. *aquilonaris*, and retain their own characteristics. Further, in the Altai Mountains, where *B. napaea* is represented by its subsp. *altaica*, a small form (corresponding to the northern f. *frigida* in Europe) was taken by Elwes (though not mentioned by him in his paper on that region (1899)) flying with *B. pales aquilonaris* in some localities in the Bashkaus valley, both insects remaining perfectly distinct. The f. *frigida* varies considerably, and owing to its small size, some examples are difficult to distinguish from the subsp. *aquilonaris*, such variation, however, is not confined to localities where the two species fly. It is worth noting that the female of *B. napaea* is dimorphic, ranging from specimens the colour of the males, through a variety of shades to practically black individuals. The female of *B. pales* subsp. *pales*, on the other hand, is monomorphic, and keeps to the orange-brown shades.

I must now briefly refer to *B. graeca* and its relationship to *B. pales*. Verity's data in this connection again seem open to question. He states that the Pyrenean subspecies of *B. pales* (subsp. *pyrenesmiscens*) is in his opinion a " final proof that *graeca* and *pales* can only be the Northern and Central exerge of a single species, considering they have blent together completely in an intermediate synexerge . . ." (1932 : 103). I am quite unable to see how subsp. *pyrenesmiscens* can be said to be a blend of *B. pales* and *B. graeca*, or even that it is completely intermediate between them. Its coloration and markings are so specialised that no visible connection with typical *B. pales* remains; morphologically, its affinities lie with the subspecies *alethea* (= *arsilache* var. Esp.) and *aquilonaris*. The coloration of the underside is suggestive of *B. graeca*; but there the similarity ends. Such statements can only make one pause before accepting Verity's further record, of specimens of *B. graeca* subsp. *brogotarus* from Mount Capelet in the Maritime Alps which " blend with *palustris*." The latter is a small, high alpine form of *B. pales* subsp. *pales*; it is always inconstant, and at lower levels (such as those localities mentioned by Verity) it becomes larger, and ceases to be distinctly characterised. Such specimens, however, cannot be accepted as transitions to *B. graeca*; most often the direction of variation is towards the parent subspecies, and when paler specimens do occur they cannot be said to exhibit any of the true characteristics of *B. graeca*. Further, it would seem most probable that Verity's specimens from Mt. Capelet belong to the remarkable form of *B. pales* which occurs throughout the Cottian and Maritime Alps. Verity's remarks would apply to it in so far as occasional individuals, indistinguishable from f. *palustris*, occur with it at high levels.

I have referred to these various points rather fully, just to demonstrate that from Verity's own standpoint the theory of a single species seems untenable, as we shall see, he is put to considerable difficulty to maintain it in practice, when he tries to classify the races as a whole. At the end of his paper he gives a check list of the *Boloria* races, and it is not too much to say that this list demonstrates that he found their classification as one species impossible. In the effort to maintain this theory, he assumes three " exerges," which he subdivides into " secondary exerges," " synexerges " and " races." The system works out as : " exerge *arsilache,*" including seventeen " races " (*arsilache, banghaasi, alaskensis, sifanica, sipora, caucasica,* etc., etc.) ; followed by " secondary exerge *pales* " with two " races " ; " secondary exerge *napaea* " ; " synexerge *pyrenesmiscens* " ; " synexerge *medioitalica,*" all subdivisions of " exerge *arsilache.*" Then comes " exerge *graeca* " including three " races " ; and " exerge *generator* " including five " races." Now it will be recalled that I have shown that, to start with, Verity used the term " exerge " as meaning " subspecies," in the accepted sense of that term ; but now he places all the recognised subspecies as lower subdivisions of an " exerge " (exerge *arsilache* race *arsilache* ; exerge *graeca* race *graeca,* etc.). His " secondary exerge " and " synexerge " are a further subdivision of an " exerge," but rank as something of greater importance than his " race " (*i.e.* exerge *arsilache* secondary exerge *pales* race *pales,* and race *palustris,* etc.). Now in all zoological classification a species is accepted as a composite unit composed of a greater or lesser number of subspecies ; and the great majority of Verity's " races " are true subspecies, in the sense that I defined (1937) as " races which, so far as is ascertainable, exclude other races of the same species from the region of their distribution." It is irrefutable, therefore, that Verity's " exerges " and " secondary exerges " as used by him in his classification are merely vague terms for a unit composed of a greater, or lesser, number of subspecies ; as such they are synonymous with " species." It is obvious, then, that the impossibility of classing all *Boloria* races under one species has compelled him to raise the term " exerge " to specific rank, and adopt the conveniently vague term " race " to replace " subspecies." The " secondary exerge " differs in no respect from the " exerge," though supposed to be a subdivision of lower rank ; the two " synexerges " (*pyrenesmiscens* and *medioitalica*) are in fact units, biologically and morphologically, of identical value with the other subspecies that Verity classes as " races " : the introduction of this term shows that he was unable to decide where the affinities of these two races lay ; from the taxonomic point of view it is synonymous with his " race."

In support of his contention that all *Boloria* races must be regarded as units of one species, Verity asserts that to split them into several would simply " mean altering the meaning of the term ' species ' and shifting it to the lower rank I have called ' exerge ' " (1932 : 103). This, however, would be an impossibility : " exerge," as usually employed by Verity, stands for " subspecies " (though in his classification he was compelled to change the value) ; in any other sense it is meaningless, for it remains impossible to define a systematic rank that would be greater than a true subspecies and at the same time less than a species, for a composite unit composed of a number of highly developed subspecies cannot be differentiated from a species. Verity ended in raising his " exerge " to replace a species, and converting the latter into a genus. His classification was tantamount to making no less than five species of this group of races : namely, " *arsilache,*" *pales, napaea, graeca* and *generator.* I have shown that on Verity's own postulates, *B. pales, B. napaea* and probably also *B. graeca,* merit specific rank, but not " *arsilache* " (subsp. *generator* does not either, though I have not dealt with it) ; this classification is in accord with such morphological, ecological, and the very few biological facts I have been able to collect. We must now turn to the vital anatomical side of the question.

In a genus like *Boloria*, where structural formation is extremely generalised, striking specific characterisation is not to be expected. This, however, does not imply that there can be no visible indications of differing specific constitutions. The problem is to distinguish between the specific and subspecific developments that may exist. It is often overlooked, when the structural features in a group of races are both generalised and very simple in nature, and the physical limitations in the existing formations do not permit differing lines of development to assume any marked characters, that in such circumstances what seems to be but a microscopic change may have just as much taxonomic value as many far more obvious deviations in less generalised groups. While, of course, complete morphologic change in an organ indicates some fundamental difference, the essential elements are stability of range in variability, and constancy of presence. These essentials lose nothing in importance by limitation in size; they are, however, much more likely to get overlooked.

I do not propose to describe the genital characteristics of each *Boloria* race here, the principal points of interest in connection with them will be given in the systematic part, but the following details of structural characterisation have, of course, been derived from a careful study of every race obtainable. I have already mentioned that I have been led to classify the *Boloria* subspecies in three specific groups, under the names of *B. pales*, *B. napaea* and *B. graeca.* I will take *B. pales* and *B. napaea* first.

In all *Boloria* species the head of the harpe is the most striking feature of the male genitalia, and it is not surprising that those who have dealt with anatomy in this genus should have, apparently, confined their attention to this one process. Unfortunately, the variability in outline that it exhibits is almost limitless; its shape is not often exactly similar in any two specimens, and frequently is asymmetrical on the two claspers. Further, so far as my experience goes, any striking form developed in one species can be found reproduced exactly in another if a sufficiently large number of specimens are examined. This fact, alone, demonstrates how extremely generalised is the structural development in the genus. A good idea of the variability of this process is given by the photographs of twenty-seven *B. napaea* (pls. 13–18) and sixty-three *B. pales* (pls. 17–28). All this variability in form is for the greater part individual, but also, to a limited extent, racial in nature; the actual shape of the head, therefore, is valueless as an indication of specific nature. But, while the contours of the outline must be disregarded, the development of the head gives remarkable indication of differing nature in another way. The head, or distal end of the harpe, bears a series of spines along the dorsal ridge; these cease just proximad of the dorsal eminence that is developed in varying degrees in most specimens. No matter what shape the head may assume, the spines are always present, and the extent of their range seems to be correlated with the length of the free, external, distal portion of the harpe (*i.e.* the head and part of the " neck " from which it springs); for they never are present until shortly after the separation of the external portion from the clasper body. Measurements show that the extent of the range of these spines in proportion to the total length of the harpe differs in each of the three species. Thus, it is greatest in *B. napaea*, more restricted in *B. pales* and very reduced in *B. graeca.* Expressed in simpler, if not quite accurate, form, the length of the head is a different proportion of the total harpe length in each species. Measurements on one hundred and seventy-eight mounts give the following results: *B. napaea*, spinal range varies from 14/30 to 19/30 of total harpe length, normal development (that shown by the vast majority of individuals) 15/30 (= 1/2); *B. pales*

10/30 to 15/30, normally 12/30 (= 2/5); *B. graeca*, 9/30 to 12/30, normally 10/30 (= 1/3). As the effective use-value of the head most probably depends on the spinal ridge, and the extent of the latter, in turn, depends on the extent of the free external portion, it would be more accurate, therefore, to take the actual measures of the free and attached, or external and internal sections of the harpe. This, however, would have to be done before the specimen was mounted, as in most mounts it is not possible to see the exact point where union ends. The unquestionable correlation between the free portion and its dorsal armament, however, justifies one in employing the data obtainable from the latter; though the measures will differ from those which would be derived from the more basic measures, the relative proportions give the same results. To some readers my figures may suggest that the differences are very slight, and inconstant, but it must be recollected that the external location of the head is a highly specialised character, peculiar to the Argynnids (see ante), and that this external portion has become amazingly elaborate in related genera. Any constant difference in the ratio between the external and internal portions, if discernible in a number of subspecies and constant in groups of the latter, indicates differences in specific nature and assumes a degree of importance on which the actual differences in terms of measurement have no bearing. Perhaps I should add that when I say " internal " in connection with the proximal portion of the harpe, in this case it is only " internal " in contradistinction to the free external portion, and not completely internal as the ventral branch is in those other genera where it is highly developed.

The difference in the lengths of the head are fairly obvious to the eye; in the great majority of cases I found I could determine the species to which a given specimen belonged merely by the look of the head. The most obvious point of difference between the two species, however, is size; it can be seen in the photographs that the genitalia in the *B. pales* races are smaller, and of lighter build than in the *B. napaea* races. The general structure is very uniform in both, and the increase or reduction in the size of any part is proportionate to the general increase or decrease. This fact at once marks the change in the ratio of the free to the attached parts of the head, as something out of the normal, and independent of the physical changes controlling growth in the associated organs. This quite discountenances the fact that in *B. pales* the greatest length of the spined area attains the average length in *B. napaea*, and the shortest, the average in *B. graeca*. In the latter the general size of the genitalia is approximately equal to that in *B. pales*; yet the alteration in the ratio is greater than that existing between *B. pales* and *B. napaea*. This is a further very important point emphasising that the development of the free, distal portion of the harpe is in no way correlated with the general dimensions of the clasper or the associated organs. The extremes in every case are few in number, compared with the average examples; and where so much individual variation is known to exist in the shape of the head, it is certain that the length must be affected to a certain extent. As the average of the ratio differs in the various groups of subspecies, it stands as a specific character; otherwise one would have to follow Verity's line and presume the existence of some taxonomic unit superior to, and including a number of, subspecies, yet inferior to the species. Further, in size the genitalia are very constant; and this is independent of the size of the individual. The size of different races varies within a species, and sometimes in a small race the genitalia also are smaller. This is most marked in *B. napaea*; but on the other hand, in some large races of *B. pales*, the genitalia are actually smaller than in smaller subspecies. On the whole, however, these changes are slight, and do not detract from the taxonomic value attaching to the size developed by each species, but rather add to it, as I will show. I have selected certain photographs to illustrate this question, and placed them together on plates 16, 17 and 18, figs. 63–80—these should be very carefully studied when reading the following paragraph.

Starting with pl. 16, fig. 63 shows the complete genitalia of *B. napaea*, a normal-sized specimen from south-west Switzerland; below it (fig. 66) is a specimen of the subsp. *altaica* from Irkut. The latter is the largest known race of the species (see pl. 33, figs. 178–183, and compare with pls. 30 and 31); it is constantly slightly larger than the typical race from central Europe. The genitalia of another Swiss example are shown in fig. 68. The difference in size between the last and figs. 63 and 66 is very slight. On pl. 17, figs. 70, 72 and 74, show three more central European specimens, while fig. 76 (pl. 18) is the subsp. *altaica* at its finest development; slightly larger than the specimen fig. 66. On pl. 17, the figs. 71, 73 and 75, show typical-sized specimens of *B. pales*. Now the two specimens (fig. 70 *B. napaea* and fig. 71 *B. pales*) were taken at the same time in the restricted locality of the " Latemar Meadow " in the Dolomites. The actual specimens are shown (*B. napaea* pl. 30, fig. 151; *B. pales* pl. 35, fig. 207), and it will be seen that there is very little difference in size between them. Fig. 72, *B. napaea* from the Val Minor, Bernina Pass, was a slightly undersized specimen; fig. 73, *B. pales* from Pontresina, was abnormally large and equal in size to the *B. napaea* with which it was flying. Fig. 74, *B. napaea*, and fig. 75, *B. pales*, both specimens taken at the same spot near Morteratsch, Bernina Pass; the *B. napaea* is shown in fig. 152 (pl. 30), the *B. pales* fig. 211 (pl. 36); the latter will be seen to be the larger insect of the two.

From such facts, which are typical for these species, one can confidently say that the difference in size of the genitalia is independent of growth, locality or conditions of existence : *i.e.* an inherent, constitutional peculiarity, which is constant in all races throughout the geographical range of the species.

On pl. 18, fig. 76 is the subsp. *altaica* of *B. napaea* and fig. 77 the small form corresponding to the Scandinavian f. *frigida*; the actual specimen is shown on pl. 33, figs. 184 and 185. Fig. 78 is an example of the subsp. *korla* of *B. pales*, one of the largest *Boloria* races known. Typical specimens of subsp. *korla* are shown on pl. 41. They will be seen to be much larger than the small form of subsp. *altaica*, and equal and even surpass the latter subspecies at its largest; yet the genitalia remain typical of *B. pales* in dimensions, smaller even than the small form of *B. napaea*. One must also note that in that small form, the heavy aedeagus and expanded wings of the phallobase are typical of *B. napaea*, compared with the slighter build of these organs in fig. 78. But even this is not all. The two remaining figures on pl. 18 illustrate two other races of *B. pales* : the subsp. *generator* (fig. 79), and subsp. *sipora* (fig. 80). The former is a large race; without equalling subsp. *korla*, it is normally larger than typical subsp. *pales* of the central European Alps; subsp. *sipora* is about the same size as the latter. The specimen of subsp. *sipora* is shown on pl. 37, figs. 226 and 227; normal-sized specimens of subsp. *generator* on pl. 42, figs. 268–271. One sees, then, that the genitalia in subsp. *generator* (which equals *B. napaea* subsp. *altaica* in size) are even smaller than in subsp. *korla*; and in subsp. *sipora*, which is almost as small as the f. *palustris* of subsp. *pales*, the genitalia are only slightly smaller than in the subsp. *korla*.

I have already mentioned the extensive individual variability which affects the shape of the head of the harpe, and how this has led to the development of racial formations in various cases; these racial characteristics will be described in the systematic part of the work, but it must be noted that they cannot be accounted for by supposed interbreeding. I have shown (1937a) in the case of a true, natural hybrid, between two species of the genus *Erebia*, that the male genital armature in the hybrids displayed a transitional condition in every important character. The racial formations developed on occasions by the head of the harpe in *Boloria* are not accompanied by other changes in the general character of the associated organs, neither do they affect the proportionate length of the external and internal portions of the harpe, proper to the species. Such variability can, therefore, in no circumstances be attributed to interbreeding.

From the anatomical point of view, then, *B. napaea* and *B. pales* may be said to differ in that the male genital armature as a whole is larger in the former, the aedeagus and its supporting wings heavier and broader, and the external, free portion of the harpe longer, in proportion to the basal portion. To these facts one must add that various races of both species occur together in numerous regions, under similar conditions, throughout Europe and Asia, without interbreeding; finally, as Reuss records (1925), the pupae of *B. napaea* are twice as broad as those of *B. pales*, although they are practically equal in length, while those of the latter and "*arsilache*" are identical. Vorbrodt also (1928) stated that owing to some differences in the larva and pupa of *B. pales* and *B. napaea* it has been suggested that they are distinct species; but he does not mention what the differences may be. Considering these facts, I fail to understand how anyone can claim that these two insects are conspecific.

Before turning to *B. graeca*, it may be as well to mention the subsp. *aquilonaris* of *B. pales*, i.e. the "*arsilache*" of so many writers. Anatomically, I am unable to distinguish it from other *B. pales* races; there is a difference in the ventral curvature of the harpe, which in subsp. *aquilonaris* (and subsp. *alethea* = *arsilache* var. Esp.) is frequently deeply concave, while in the other subspecies it is much flatter. This difference, however, is purely subspecific in nature, for it varies in degree in the vast majority of individuals and even disappears at times. The fact that this feature occurs in subsp. *alethea* also, might be argued as a reason for separating these two very similar races as a specific unit. But in fact this ventral curvature occurs occasionally in many of the other *Boloria* races: for example, *B. napaea* subsp. *nearctica* (pl. 15, fig. 61); subsp. *napaea* (pl. 17, fig. 70); *B. pales* subsp. *pales* (pl. 21, fig. 95); subsp. *pyrenesmiscens* (pl. 28, fig. 140) etc. From this it is clear that the abnormal curvature is an individual variation which occurs with peculiar frequency in the subspp. *aquilonaris* and *alethea*, but not constantly; otherwise the genitalia in these races are typical of the normal formation prevailing among the *B. pales* subspecies.

As I have already remarked, the chief reason why many English collectors have claimed specific rank for subsp. *aquilonaris* is that it is a swamp insect; and subsp. *pales*, it is assumed, is not. There is no doubt that both subsp. *aquilonaris* and subsp. *alethea* are very susceptible to environment, and in the wettest localities develop their finest size and deepest coloration, especially on the underside. Immediately they come under the influence of drier surroundings they lose both size and colour, and in fact show every indication of reversion to the subsp. *pales*. In contrast to this, *B. napaea*, which is at home in both wet and dry localities, appears unaffected to any observable degree by environment. *B. pales* subsp. *pales*, on the other hand, responds to environment nearly as readily as the subsps. *aquilonaris* and *alethea*. As a general rule subsp. *pales* does not inhabit such extremely wet localities as the latter; but the wetter the locality, the more vivid the coloration, especially on the underside. This susceptibility to environment has led to the development of a very unstable form, in the central and southern Alps, to which the name "*palustris*" has become attached. This form is a high-level form, frequently found on marshy ground and consequently often brilliant in colour; but it also occurs at lower levels and on dry ground, and under such conditions gains in size but loses in colour. It can be said that, as a rule, any contact with moisture coupled with lower altitude produces an approximation to subsp. *pales* (i.e. greater size and bright coloration); while increasing altitude plus moisture tends to reduction in size coupled with richness in colour, lower altitude plus dryness to increase in size and loss of colour. The result of this response to environment makes it frequently very difficult to say whether the race of a given locality is subsp. *pales* or the f. *palustris.* The subsp. *pales* is of course a true subspecies, and therefore occurs as a pure race in many localities, especially in the eastern Alps; but the f. *palustris* being only a form (or incipient subspecies) never occurs to the exclusion of the parent subspecies (*i.e.* subsp. *pales*). Consequently, the two are always found where f. *palustris* occurs, but the proportion of either, or of transitional specimens, varies in each locality, and may even do so from day to day. In view of these facts, the habitat of the subsps. *aquilonaris* and *alethea* ceases to be a factor of particular importance, for, as we have seen, change of environment affects them and subsp. *pales* in an exactly similar manner. Were subsp. *pales* and subsp. *aquilonaris* brought into one locality, of less extreme moisture than is normal to the latter, there is every reason to suppose that it would only be a question of time before the two would have developed an identical appearance.

I have not come on any more modern account of the larvae of these races than Staudinger's (1855), when he stated them to be identical; Reuss (1925) makes the same remark about the pupae. All available data then, morphological, ecological and biological, point to the conclusion that the subspp. *pales, aquilonaris* and *alethea* are races of one species.

Of *B. graeca* less need be said. Morphologically, it is the most distinct of the three species of this generalised genus. I have already shown that the spinal range on the head of the harpe is less than in either of the other species. So far as the comparison with *B. pales* is concerned, however, the actual difference is less than the photographs on pl. 29 might suggest, and as I have only dissected ten specimens of *B. graeca* and its races, it is quite possible that a larger number might give a slightly greater spinal range, for, judging from the few tests I made, there seems to be a greater difference between the spinal range and the length of the actually free portion of the harpe. This point, however, is not of vital consequence, considering the other characters exhibited by *B. graeca.* As I have already noted, the genitalia of *B. graeca* are, as a whole, as large, and often larger than in *B. pales*, yet there is a marked reduction in the size of the wings of the phallobase, which are both slightly shorter and decidedly narrower. This fact is further enhanced by the proportions of the aedeagus, which is reduced in a manner disproportionate both to the reduction of the phallobasic wings, and the general development of the periphallic organs; for it is practically equal in size to the aedeagus in some *B. pales* races. It also varies in size occasionally, without any corresponding alteration in the development of the wings; a most remarkable fact, for, as I have already shown in part II, there is a distinct correlation between the development of the aedeagus and its supporting wings in all other genera. This exception to an otherwise invariable relationship between two closely connected structures marks the *B. graeca* races as standing decidedly apart from all others. In *Argyronome laodice* a disproportionate development in the size of the phallic organs, as contrasted with the periphallic, has taken place; but this is the sole example I have come on in the tribe, and it is not an exact equivalent of the change in *B. graeca*; for in *A. laodice* the immense enlargement which has taken place in the phallic organs as a whole is absolutely proportional in every structure, the relative dimensions of the aedeagus and the phallobasic wings remaining unaffected.

Data respecting localities and distribution are very limited, and have little bearing on the question of the specific standing of *B. graeca*, but in view of the remarkable structural characteristics just described this matters little, for it would clearly be impossible to include the three highly specialised *graeca* races in either of the other specific groups of races. Verity's observation (1932 : 103) that in some localities in the Maritime Alps *B. pales* f. *palustris* produces a " complete transition from individuals very similar to *palustris* to others, notably of the female sex, exactly similar to Staudinger's figure of *graeca*," can only be the result of a false impression gathered from a too limited material of the variable form of *B. pales* from the Cottian and Maritime Alps, which, as I have previously noted, exhibits some of the superficial characters of both subsp. *pales* and subsp. *pyrenesmiscens.* Some of the females closest to the latter must have been mistaken by Verity for *B. graeca.* He further adds that specimens from Vallasco above Valdieri belong to an " intermediate race." These specimens had previously been recorded as " ssp. *brogotarus* " (Turati and Verity 1911), but in all probability they belong to the form of the Maritime Alps, now correctly referred to by Verity as an intermediate race, and not to any form of *B. graeca.* Colour and markings are an unreliable guide to relationship at any time, and especially so in species which are as susceptible to environment as *B. pales* is known to be, and also probably *B. graeca* (judging from variation exhibited by Balkan specimens) is. One cannot overlook that in his classification of the *Boloria* races, Verity, trusting to superficial appearance, placed sixteen subspecies under " exerge *arsilache* " as distinct from *B. pales* and *B. napaea*, and claimed to have demonstrated a distinct line of origin for them; yet, as my morphological data show, only two of the sixteen races are correctly placed; of the remainder, four (*nikolajewski*, *isisoides*, *nearctica* and *alaskensis*) are races of *B. napaea*, nine are races of *B. pales*, and the remaining one (*sachalinensis*) I have not been able to examine. From this one sees how necessary is some guide from a knowledge of the more stable structural elements, when endeavouring to establish the relationship between such generalised races.

It is a well-known fact that absolutely distinct species of the same genus, if they occur in the same locality, sometimes tend to develop a superficial likeness to one another; a familiar example of this appears in the Laquintal on the Simplon Pass, where specimens of *Erebia epiphron* which have a decided resemblance to *Erebia christi* are not uncommon. Such specimens rarely occur in other localities; but though they are often responsible for misidentifications by collectors, it would be quite inaccurate to describe them as transitions to *E. christi.* It is interesting to know that *B. pales* and *B. graeca* (as the case may be) respond as readily to local conditions in this south-western area of the Alps as farther north and east; this, however, does not alter the fact that it would appear to be practically impossible that true transitions, such as exist between *B. pales* subsp. *pales* and the f. *palustris*, could ever occur between any races of *B. pales* and *B. graeca.*

I do not think that any lepidopterist who has followed the foregoing discussion with the aid of the plates will question the specific discreteness of *B. pales*, *B. napaea* and *B. graeca*. I have also dealt with the claim that "*arsilache*" should be regarded as distinct: it does not seem necessary then to deal further with the possibility that other races, now included under *B. pales* or *B. napaea*, are distinct. The structural details already given are equally applicable in their case. It may, however, be as well to mention in conclusion that the "*arsilache*" of most writers really includes two subspecies: *i.e.* the subspp. *aquilonaris* and *alethea*, the latter being the true "*Papilio arsilache* var." of Esper. These two subspecies are in many respects so closely related that there is some ground for supposing one to be a form of the other; but a careful study of all available material failed to prove that the two ever occur in the same locality; and though it may be difficult at times to identify the race of a given locality, it is quite impossible to unite those of other localities.

V. THE GENUS *BOLORIA*.

Genus *Boloria* Moore, 1900.

Genotype *Papilio pales* [Denis and Schiffermuller] 1775.

I. *Boloria napaea* (Hoffmansegg).

Synonymy :—Papilio napaea Hoffmansegg, 1804, Illiger, *Magazin für Insktenk.* **3** : 196; *Papilio isis* Hübner, 1800, *Sam. eur. Schmett. Pap.* pl. 7, figs. 38, 39 male, 1804, *Pap.* pl. 110, figs. 563, 564 female, p. 9 (primary homonym of *Papilio isis* Drury, 1782, *Ill. Nat. Hist.* **3**, index and 8; *Papilio isis* Thunberg, 1791, *Ins. Suecica* (2) : 31; *Papilio isis* Fabricius, 1793, *Ent. Syst.* **3** (1) : 124). *Papilio dirphya* Hoffmansegg, 1806, Illiger, *Magazin für Insektenk.* **5** : 180.

Verity (1932) seems to have been the first to note how incorrect it is to restrict the name "*napaea*" to those females of the species that are suffused with violet, as was done by Hübner. Hoffmansegg substituted "*napaea*" for *isis* Hb., the latter being a primary homonym many times over (see above), so Hübner's later action in restricting *napaea* to a female variety of his own *isis* was quite unsupportable. Hoffmansegg, who even at that early period recognised the necessity for avoiding homonyms in nomenclature, later changed his *napaea* to *dirphya*, when he found that he had overlooked Esper's *napaeae*. Verity maintained (1932) that this change was uncalled for, as Hoffmansegg's and Esper's names, in spite of their close similarity, had the validity of two different names. I agreed with his point of view, but as some writers had adopted *dirphya*, I referred the question to Mr. A. M. Morley, O.B.E., who is a classical expert as well as an entomologist, in order to make quite sure that Hoffmansegg's *napaea* would not fall under Article 35 (section a) of the International Code. After a careful study of the matter, Mr. Morley informed me that he concluded that the names *Papilio napi* L. and *P. napaeae* Esp. were derived from the Latin *napus* (turnip), but that *napaea* Hoff., as a race of *B. pales*, seemed to have no connection with turnips, and was probably derived either from the adjective *napaeus* (belonging to a dell), or the Greek *napaea* (a dell nymph); the former of course coming from the latter. It seems fairly certain, then, that Esper's and Hoffmansegg's names cannot be regarded as "of the same origin and meaning," and therefore do not interfere with each other under Article 35; hence, *napaea* Hoffmsg. remains the valid name of the species.

Composition of species :—Six distinct subspecies are known, and it is suggested that there is a seventh, but at present the requisite material is not available to establish it; two of the subspecies develop local forms, which is of particular interest as two of these forms correspond very closely and occur under similar conditions, though widely separated geographically. The female is dimorphic in each subspecies.

(1) *B. napaea napaea* (Hoffmsg.).

Pl. 30, figs. 148–157; pl. 31, figs. 158–167.

Original description :—Hoffmansegg merely applied the name to Hübner's figures; his note runs as follows: "Isis. T. 7. f. 38. 39.-T. 110. f. 563. 564. Napaea n." As he makes no reference to locality, the race of the Tyrolean Alps remains the typical one, that being the locality that was given by Hübner. Verity (1932) comments on the fact that Hübner also stated he had received the same insect from the Savoy, and says that this evidently was a mistake, and the insect Hübner was referring to must have been the form *palustris* of *B. pales.* I cannot see why Verity came to this conclusion, as absolutely typical subsp. *napaea* are abundant in many localities in the Savoy and adjoining Swiss Alps.

Genitalia :—Pl. 13, figs. 45–50; pl. 14, figs. 51, 53; pl. 15, fig. 60; pl. 16, figs. 63, 68; pl. 17, figs. 70, 72, 74. The genitalia of *B. napaea* have been fully described already in parts II, III and IV; it will be sufficient to note the chief characteristics here without further comparison.

Large size, constantly greater than in the *B. pales* or *B. graeca* races; phallic organs correspondingly developed; of heavier build than in the other species: average range of spinal development on the head of the harpe equal to half the total length of that structure. Individual variability is great in the head of the harpe, though not greater than in some races of other species. A very remarkable, and unusual, variation in the form of the claspers is shown on pl. 14, fig. 51. Here the ventral line of the claspers is sharply angled centrally, instead of forming a gentle curve. This angulation occasionally occurs in both *B. pales* and *B. graeca*, but apparently is never so pronouncedly developed.

Identification :—There is no single character which can be relied on to distinguish the typical subspecies of *B. napaea* and *B. pales* with certainty; and it will always be necessary to look for a combination of characters to identify a specimen. Also it must not be expected that all characters will be present in every specimen. All the same it is by no means as difficult to distinguish the two species as this might lead one to expect.

B. napaea is, normally, larger, its wings are broader and more rounded (less angular), and the red ground-colour of the underside of the hind-wings is either browner or more yellow in tone than in *B. pales.* Actually this colour in *B. napaea* is much browner than is usually supposed, and it generally ranges from a yellow-brown to orange-brown, while in *B. pales* it keeps more in the red-browns, with a mixture of purple shades. The difference in size, shape and colouring, though difficult to describe, is often so marked that it is no unusual thing to be able to distinguish the two species when flying together. The females are easier to distinguish than the males, owing to the dark suffusion on the upperside that is so frequently present in *B. napaea*, but never in *B. pales*; while the non-suffused females are usually distinguished by the size and shape, as well as the absence of reds or purple shades on the underside of the hind-wings, and the greater prevalence of yellow and green. The small details of the pattern are very helpful. On the upperside of the fore-wings, in every species, there runs a row of long and narrow black spots, from the costa to the inner margin, just outside the discoidal cell (= median row); outside this row there is a second, composed of spots that are more square, or rounded, in shape (= submarginal row). In the median row the spots stretch lengthwise from nervure to nervure; in the submarginal row they do not touch the nervures. In *B. napaea* the second spot of the median row (from the inner margin, between nervures 2 and 3) is set well away from the discoidal cell; in *B. pales* this spot is quite close to the cell, and very often actually touching it, especially at the upper end. Further, the spots of the median row in *B. napaea* are usually much narrower, more linear, than in *B. pales*. The spots of the submarginal row are more variable, but very frequently they are somewhat rounded in *B. napaea*, while they tend to be flattened on their outer edges in *B. pales*. Finally, in *B. napaea* the markings of the underside are inclined to blend, and the coloration is soft; in *B. pales* the pattern is very sharply defined, and the coloration bright, with a decided inclination for all the dark markings to be accentuated.

Individual variation is prevalent in both species, and many aberrations have been described. As a rule abnormal markings do not add to the difficulty of identification: changes in size, however, are more likely to do so, and specimens like fig. 152 (pl. 30), when taken flying with *B. pales*, may cause mistakes. If this figure, however, be compared with fig. 211 (pl. 36), which shows a specimen of *B. pales* from the same locality, in spite of the similar size and shape, the very linear spots of the median row and the more rounded ones of the submarginal row give the specimen a different look from fig. 211. Further, though the reduction in size has cramped the markings in fig. 152, the uppermost end of the second median spot is still separated from the cell by a gap of its own width; whereas in fig. 211, this spot practically reaches the cell at its uppermost corner, though less distinctly so than in many cases, as can be seen by the other figures on plates 35 and 36. The normal position of this second median spot in *B. napaea* is clearly seen in the figures above and below fig. 152. The underside of this specimen is typical of the species, both in colouring and lack of brilliance; but from the upperside alone it is possible to identify such specimens. Two other very remarkable aberrations of the male are shown on pl. 30 (figs. 156 and 157); I was able to identify each of these as *B. napaea* before catching it. It is worth noting, however, that in fig. 156, in spite of the altogether phenomenal development of the spots of the median row, the second spot retains its normal position and does not approach the cell. The same feature can be made out in fig. 157, in spite of the heavy suffusion of black all over the fore-wings. This suffusion is of course most unusual in the males, though frequent in the females. The undersides of these two aberrations are perfectly normal. The great range of the shades of colouring of the upperside in the females is a well-known characteristic of the species. Many females are paler than the normal males, as in fig. 153, from the Karer Pass, and fig. 158 from the Savoy Alps; or just about the same (fig. 155), or slightly darker red-brown as fig. 166 (pl. 31), from Norway. The melanic forms develop a black superscaling that can be present in any degree, from a slight dusting of dark scales to such a dense coating that the specimen assumes a completely black appearance. This black superscaling tends to take a more or less pronounced green, or purple, reflection, that can attain a lustre of extreme brilliance. These beautiful colours are due to refraction, and collectors may be warned not to relax their specimens, for if they are set when the least damp the scales will be compressed and will remain so after the specimen is taken from the setting board, and most, if not all, of the magnificent, iridescent colouring will have disappeared.

The females developing this suffusion have usually been referred to as aberrations, which is quite inaccurate, for they often constitute a high percentage of all the females in a given locality. The use of the name "*napaea* Hb." for these dark females is, of course, wrong, and as all other names given to melanic forms refer to particular aberrations, Verity was quite correct in introducing names to cover the two types of melanic females :—

Subsp. *napaea* f. *atroviolacea* Vty.; Pl. 31, fig. 162 : f. *atroviridans* Vty.; Pl. 31, figs. 159, 160.

Synonymy :—Boloria pales secondary exerge *napaea* Hoffmsg. f. *atroviolacea* Verity; and f. *atroviridans* Verity; 1932, *Dtsch. ent. Z.* "*Iris*" **46** : 108; *Papilio napaea* Hübner, 1819, *Samml. eur. Schmett. Pap.* pl. 151, figs. 757, 758; 1833, (Geyer) *Pap.* pl. 195, fig. 964 (primary homonym of *Papilio napaea* Hoffmansegg, 1804, Illiger, *Magazin für Insektenk.* **5** : 180).

Original description :—"As to the dark form of the female, I do not think that, apart from melanic aberrations, any name exists in the *Boloria* genus for it and so I propose that of *atroviolacea* for the form such as the one of Hübner's fig. 757–8 which is shot with violet, and that of *atroviridans* for the form, such as the one of his figure 964, which has a more greenish or bluish hue."

The introduction of these names finally fixes the unsuffused form of the female, similar in colour to the male, as the typical one. As a rule f. *atroviolacea* produces the darkest forms of all, such as fig. 162; in f. *atroviridans* the ground-colour is rarely so completely obscured. Fig. 160 (pl. 31) is the darkest specimen of the latter I have seen. Fig. 159 (pl. 31) shows one of the unexpected features which appear in aberrations of this species, for though it is an extremely dark example of f. *atroviridans*, the marginal row of pale spots on both fore and hind-wings are not only enlarged, but white in colour, and quite free of the superscaling that spreads completely over the rest of the wing.

The coloration of the underside in the female is as variable as that of the upperside. Broadly speaking, the ground-colour of the underside of the hind-wings may be either red-brown, yellow, or pale green. All three shades vary extensively, and appear in conjunction with any shade of coloration of the upperside. In addition, the actual pattern varies in definition to a considerable extent; fig. 167 shows a very well-marked type, figs. 163 and 161, two of the more obliterated forms. Before leaving the subject I would emphasise again that the typical orange-brown females without suffusion are often just as abundant as the dark forms, and can show a surprising range in the shade of coloration; many writers have stated that all *B. napaea* females are dark, a curious mistake that probably arose owing to Hübner's use of the name.

Habitat and Period of Flight :—Subsp. *napaea* appears capable of maintaining itself in very varied habitats. In the Alps it has a vertical range of about 3000 feet, but is most frequently found between 5500 and 7500 feet. Only very rarely does it occur below the 5000-foot level. Tutt (1907b) records it at about 4600 feet in the Goeschenen district, and I have taken it myself about that level in the neighbourhood of Barmaz in the Valais. There are many records of very low levels in the eastern Alps, such as Osthelder's (1925) of 3250 feet, in southern Bavaria, and Hoffmann and Klos's (1914) of 3900 feet, in the Styrian Alps; but they all give these levels for "*pales*," and, though likely, one cannot be certain if they cover *B. napaea* also. The other extreme must be about 8000 feet. I have taken it at 7800 feet, on the Schafberg above Pontresina, and just a little lower on the eastern side of Piz Albris. There are records of "*pales*" from altitudes over 9000 feet; but again, there is no means of telling if these all refer to *B. pales*, or whether some may not include *B. napaea*. In the upper levels of the coniferous zone, and the first 500 feet above it, the species occurs in greatest profusion. Anywhere where there is a rich alpine vegetation, in wet or dry localities, one may find it, even in open glades in the forests, quite cut off from the open country by great stretches of forest. The flight period has been variously recorded as from June to September, but there is much uncertainty as to the species to which these records apply. September, though perhaps unusual, is by no means impossible, for on occasions *B. napaea* does not emerge until late July; *e.g.* in 1937, near Mallnitz in Carinthia, I found the first male (one specimen only) on 28 July. The duration of the flight seems to be six to seven weeks, so that when emergence only starts in late July, it would be nothing abnormal to find the species still on the wing in early September.

Distribution :—Considering how much has been written about this species, and that the subsp. *napaea* is confined to Europe, it is strange how little accurate information on its distribution is available. At present I find it impossible to state the limits of the geographical range of the subspecies with certainty. Described from the Tyrol, it is apparently widely distributed and abundant in the north, but extends very little further in that direction. Osthelder (1925), quoting Hellweger, says it is abundant in the Austrian Tyrol, but in southern Bavaria he records it only from the Allgauer Alps and the Berchtesgaden district. In the south Tyrol it is also frequently mentioned, and well distributed in the Dolomites, where Schawerda (1924) states that it is the most usual form, *i.e.* more frequently found than *B. pales.* This is not my experience, for in the Karer Pass district I came on *B. napaea* only in one very restricted locality (the " Latemar Meadow "), while *B. pales* was present in many. Exactly how far east it extends is doubtful; it is fairly widespread in Carinthia, but though mentioned from a few localities in Styria, Hoffmann and Klos (1914) seem doubtful of these records, and say they have never come on the species in the Styrian Alps. East of Styria I know of no records excepting that of Heyne (1895), who states that it is found in the Tatra, but this needs confirmation. Turning west, it occurs in the Brenner Pass district; in the Oetztal Alps, Kitt (1912), Cooke (1937), etc.; the Vorarlberg, Tutt (1910), Cooke (1938); and south to the Ortler Alps, Cooke (1927). In Switzerland even, data are wanting. It is very abundant in the Rhaetian and Lepontine Alps, occurring almost everywhere at suitable levels. From the Alps north of the valley of the Upper Rhine I have no reliable records, and, apparently, the species is wanting in most districts of the Bernese Alps. Dadd (1925) records that at Wengen and the Scheideck he found only *B. pales*, but some very old records suggest that *B. napaea* may occur in the Hasli Tal district. At the south-western end of the Bernese Alps I have found it in the mountains to the west of the Rhone Valley; in this region it is to be expected that it also occurs farther to the north and east of the valley. Between the head-waters of the Rhine and the Rhone, it occurs in the St. Gothard Alps (Tutt, 1907b and 1908a); but how far to the north it extends in this area is not known. South of the Rhone it appears to be abundant throughout the Pennine Alps, and from that chain extends into the Mt. Blanc district, and westward throughout the Savoy Alps. In France, south of the Savoy, *B. napaea* has been recorded from a few localities in the Graian and Cottian Alps, and from the northern limits of the Maritime Alps. The most southerly record that I have is Tutt's (1907a) at Allos; as the country to the south of Allos has been very extensively collected in, it seems scarcely possible that if *B. napaea* occurred there it could have escaped notice. That the few records in the Graian and Cottian Alps do not in the least represent the real range of the species in those regions there can be no doubt; one has only to recall how abundant and widely distributed it is in the neighbouring Savoy Alps, to realise this. The records in this case are clearly only an indication of those localities which are most favoured by collectors. The extreme limit of the western range of subsp. *napaea* is in the eastern Pyrenees, and this locality is at the same time the most southerly point the race is known to attain. The occurrence of the species in the Pyrenees does not seem to have been previously recorded, but there is a small series of specimens from those mountains in the Oberthür collection. All the specimens came from two districts, and are labelled either " Lipaudère et Pla-Guilhem, et Col de la Roquette," or " Vallée d'Eyne et Cambre d'Aze." With them there were numerous specimens of *B. pales* subsp. *pyrenesmiscens* from both districts, yet one further interesting example of how various races of *B. pales* and *B. napaea* so frequently exist together on the same ground.

B. napaea does not occur in the Jura, Vosges or Black Forest; nor apparently in districts north of the Bavarian Highlands, in central Europe. It is widely distributed in Scandinavia, however, and probably occurs in Finland also, though I have not as yet obtained any reliable records from districts in the latter country. There are, as usual, many references to " *B. pales* " and " *arsilache* " flying together in various localities in Finland, which makes it more or less certain, in view of the similar records from Scandinavia that I have been able to check, that the " *pales* " would prove to be *B. napaea* if one could examine them.

In southern Scandinavia subsp. *napaea* is abundant in the Dovre Fjeld, and though at present I have not come on any specimens from southern Sweden, there is no reason to doubt that it occurs there, for it does in central Sweden. In the extreme north the small arctic form occurs at Abisko on Lake Tornea, which implies the presence of the typical subspecies also, though of course only in restricted and varying numbers. For the same reason occasional specimens of subsp. *napaea* are found far north in Lapland; there are a typical male and female in the British Museum from 70° 23′ N. lat. in Finmark, which must be near the most northerly limit of the range of the subspecies, and possibly the most northerly region attained by any race of the species.

Subsp. **napaea** f. **frigida** form. n. Pl. 32, figs. 168–177; genitalia pl. 14, figs. 52, 54, 55, 56; pl. 15, figs. 57–59.

An arctic form, principally distinguished from subsp. *napaea* by its small size; the markings and coloration remaining more or less normal. There is a tendency to develop a slightly more angular wing formation, a characteristic that seems to accompany a reduction in size in the Central European specimens also (cf. fig. 152, pl. 30). There is also a tendency for the black markings on the upperside to become heavier, giving some examples a likeness to *B. pales* subsp. *aquilonaris*. This can be seen in marked degree in the male (fig. 170, pl. 32) and the female (fig. 175, pl. 32). The underside in such specimens, however, retains the typical *napaea*-pattern and colouring, the ground-colour of the hind-wings being a paler, brown-red tone, without any trace of the claret-colour that so often is a feature of the subsp. *aquilonaris*; all the submarginal markings are pronounced, and fill up the area between the central band and the margin of the wing, much more completely than in the latter.

Genitalia:—The genitalia of this little form are slightly smaller than these structures at their greatest development in the subsps. *napaea* and *altaica*, but, as comparison of the photographs will show, the reduction in size is not constant, and does not in the least affect the heavier type of development of the phallic organs that distinguishes the species from *B. pales.*

Distribution :—The f. *frigida* is principally found north of the Arctic Circle in Europe; it occurs occasionally, however, as far south as the Dovre Fjeld. I have seen it from Abisko (N. Sweden), and Rundhaug and elsewhere in the Maalselven district (N. Norway). Mr. Haig-Thomas informs me (*in litt.*) that in the latter district the insect is widely distributed over the watershed between Norway and Sweden and flies in July.

The holotype (pl. 32, figs. 172, 173) came from Maalselven; it is in the Warren collection: paratypes (pl. 32, figs. 174, 176) in the Haig-Thomas collection.

(2) *B. napaea altaica* (Gr.-Gr.).

Pl. 33, figs. 178–183.

Synonymy :—*Argynnis pales* (*isis*) var. *altaica* Groum-Grshimaïlo, 1893, *Horae Soc. ent. Ross.* **27** : 128; *Argynnis arsilache* f. *isisoides* Heydemann, 1920, *Dtsch. ent. Z.* "*Iris*" **34** : 270.

Original description :—" Alis ♂-ris subtus, ♀-ae supra et subtus pallidioribus, obtusioribus.

" In montibus Altaicis (fluv. Kara-Kabal) anno 1888 a Dom. Suwortzev detecta."

Genitalia :—Pl. 16, fig. 66; pl. 18, fig. 76. The genitalia are typical of the species and do not develop any subspecific peculiarity.

Identification :—The most striking characteristic of this subspecies is its great size. Although specimens of subsp. *napaea* can be found that are almost as large, especially among the females, on the average subsp. *altaica* is distinctly the larger of the two. In colour it is duller on the upperside, but the chief difference lies on the underside of the hind-wings, the ground-colour of which has a distinctly yellow-brown tone in the males, and is quite yellow with slight traces of brown in the females. The female shown in pl. 33, fig. 182 is a greenish-yellow colour on the underside. On the upperside the females are almost as variable as they are in subsp. *napaea*; Elwes (1899) notes that they can vary from the darkest to the palest forms as in Europe. Fig. 182 shows a moderately dark example that had a slight violet lustre.

I include the f. *isisoides* Heydemann as a synonym of this subspecies, as it is evident from Heydemann's notes on the *B. pales* races (1920) that he did not know the subsp. *altaica.* He deals with *B. napaea* as " *isis* Hb." and states that it is an aberration of *B. pales* in the Alps, and a subspecies in the Altai; apparently assuming that the European and Asiatic insects are identical. In his description he contrasts his Sayan specimens with *B. pales* subsp. *banghaasi*; but makes no mention of the subsp. *altaica.* His description runs as follows :—

> " f. (subsp.) nova, der vorigen [3] nahestehend, von den Sajanbergen; Useite fast ganz ohne Silber, alle Zeichnung verschwommen, mit einer auf der gleichförmigen Useite besonders auffallenden zusammenhängenden, rotbraunen, verwaschen begrenzten Binde; Useite der Hfl der ♀♀ heller, markanter, mit 3 bis 4 silbernen Randpunkten; Oseits dunkler übergossen."

There is nothing particular in this description to distinguish *isisoides* from the subsp. *altaica* : the reference to the silver spots of the underside, " almost

[3] = *banghaasi* Seitz.

quite without silver," suggests variability among Heydemann's specimens. These silver spots vary in the Altai specimens also, being much more marked in some individuals than others. Elwes (1899) refers to specimens taken by Lederer in the Sayansk mountains as being very like his own from the Altai. The specimens in the Elwes collection, which I take to be those he was referring to, are labelled "Irkut" (I have figured two, pl. 33, fig. 180 a male, and fig. 183 a female). The male from the Altai, pl. 33, fig. 179, shows less clear silver spotting than the Irkut male. It might be suggested that these Irkut specimens came from the Baikal Mountains, but Elwes, who procured them, was evidently satisfied that they came from the Sayan ranges. But even if these specimens should have come from the Baikal Mountains, their presence there makes it probable that the race of the Sayan ranges would be the same, and there is nothing in the description to suggest otherwise. Finally, one must recall that Heydemann thought the Altai race was the typical subsp. *napaea*. In spite of some uncertainty as to the exact locality of Elwes's specimens then, I feel no doubt that the Sayan race is the widespread one of the Altai.

Distribution, Habitat, etc. :—The subspecies has usually been supposed to be confined to the Altai Mountains; but Staudinger (1886) also added the Tarbagatai Mountains, which of course are a considerable distance to the south of the Altai. In the latter, Elwes states (1899) that the insect was very abundant after the middle of July, from 6000 to 7000 feet, in "marshy meadows above timber line." The specimens from Irkut, which I have already mentioned, show that the race extends far to the east; it therefore has a great range, and may be expected to be found in intervening regions.

Subsp. **altaica** f. **frigidalis** form. n. Pl. 33, figs. 184, 185.

Genitalia :—Pl. 16, fig. 65; pl. 18, fig. 77. The general size of the genitalia in this little form is somewhat less than in the parent subspecies, but the heavy development of the aedeagus, wings of phallobase, and saccus, will be noted, and can be contrasted with the corresponding organs in the giant subsp. *korla* of *B. pales*, which are figured on the same plate (fig. 78).

Identification :—This form differs from f. *frigida* of subsp. *napaea* only in the colour of the underside; it is, however, necessary to give it a separate name, as it is more than probable that both forms will eventually supersede the parent subspecies in their respective localities, and have to be recognised as distinct subspecies themselves. Further, it is of great interest to mark by separate names the fact that, in spite of their similarity, these forms have been evolved from different races.

The ground-colour of the underside of the hind-wings in f. *frigidalis* is browner than that in subsp. *altaica*, and strongly tinged with purple. In the female this purple is darker, and obscures all red-brown tones. This coloration distinguishes f. *frigidalis* from f. *frigida*. The two subspecies (*napaea* and *altaica*) are more or less similar in their general appearance, but differ in the coloration of the underside, and in size; the two forms do likewise, but the difference in colour is more accentuated. Type in British Museum (Nat. Hist.).

Distribution :—The only specimens I know of are those taken by Elwes in the "Tchuja Mountains, S.E. Altai" (*i.e.* S.E. of that part of the Altai range that is in Russia, not of the main range in Mongolia), and from Arasan at 6000 feet, taken by Lederer. Elwes took typical subsp. *altaica* in the Tchuja district also, at the same date as the f. *frigidalis*, which leaves no doubt that the two occur together.

(3) *B. napaea nikolajewski* (Heydem.)

Pl. 33, figs. 186, 187.

Argynnis arsilache f. *nikolajewski* Heydemann, 1920 (Bang-Haas undescribed), *D. ent. Z.* "*Iris*" **34** : 271.

Original description :—"f. (subsp.) *nikolajewski* B.-Haas *in litt.*; noch nicht in die Literatur eingeführte, oseits sehr helle, doch scharf schwarz gezeichnete Form, nicht so dick wie *banghaasi*; useits ähnlich der vorigen, doch mit deutlicher Silberzeichnung, ohne die deutliche dunkle Binde der Hfl."[2] (In the above, "der vorigen" refers to *isisoides* Heydem.)

Genitalia :—Pl. 16, figs. 67, 69. I have had only one specimen of this race to examine; it proved to be typical of the species, but showed an unusual degree of curvature of the ventral edge of the head of the harpe. Should this prove to be a more or less constant character of subsp. *nikolajewski*, it would demonstrate its affinities with the subsp. *nearctica*, for the few specimens of the latter that I have examined exhibited this curvature also, though not in quite as extreme a manner. In the subsps. *alethea* and *aquilonaris* of *B. pales*, there is, as already noted, a tendency to develop a similar curvature of the harpe head, but as a rule it is less pronounced.

Identification :—Although Heydemann's description is very short, it is remarkable for the manner in which it agrees with Holland's description of subsp. *alaskensis*. Both writers stress the bright colour of the upperside, and the sparse, black markings. Further, if the fig. 186 is compared with that of subsp. *alaskensis* given by Gibson (1920 : pl. V, fig. 5), it will be noted that the two figures differ only in size, *nikolajewski* being decidedly the larger. The underside of the hind-wings is uniformly reddish in tone, showing little contrast, and the markings lack sharpness of outline. The agreement with subsp. *alaskensis* is, therefore, very close, but the difference in size seems to justify keeping the Asiatic race under a separate name.

Distribution :—One can assume, on account of the name, that *nikolajewski* was described from specimens taken somewhere near Nikolayevsk at the mouth of the Amur River: Heydemann gave no locality with his description. One of the two males in the British Museum came from the Elwes collection, and is labelled "Schigansk, Jakutsk, 25 June 1901". Shigansk is on the Lena, just north of the Arctic Circle; the race therefore extends over a considerable area in Siberia, and there can be little doubt that it will be found in localities between these two extremes. There is nothing to show how far to the west it may extend.

(4) *B. napaea nearctica* Vty.

Pl. 34, figs. 188–191.

Synonymy :—*Boloria pales* exerge *arsilache* race *nearctica* Verity, 1932, *D. ent. Z.* "*Iris*" **46** : 104; *Argynnis pales* Elwes *nec* Schiff., 1903, *Trans. ent. Soc. Lond.* **1903** : 241; *Argynnis pales* (northern race) Lehmann, 1913, *in* Seitz, *Macrolep.* **5** : 423.

Original description :—Verity notes (*loc. cit.*): "*alaskensis* Holl., from central Alaska, and the distinctly different race from north-eastern Alaska, described by Lehmann in Seitz's *Fauna Americana* : 423, which can be distinguished as race *nearctica* . . ."[3]

Lehmann's description, referred to by Verity above, is as follows :—

"Specimens from north-eastern Alaska (69° 40′ N. Lat. and 141° W. Long.) have in the ♂ the ground-colour bright fulvous, with the black markings moderately heavy, the fore-wings dusted with fuscous at the base, the hind-wing broadly shaded with greenish-black as far as the apex of the cell and nearly to the anal angle. Both wings densely clothed with hair in the inner half. Underneath it resembles *eupales* Fruhst. (Vol. I, pl. 68*b*), in the uncommonly variegated markings of the hind-wings. Fore-wings light fulvous, somewhat paler distally, with reddish-brown dashes at the apex and on the upper part of the termen, the black markings very faintly showing through from above. Hind-wings cinnamon-brown, marked with greenish-yellow spots at the base, a strongly denticulate and deeply notched median band of yellowish-green colour, and the termen similarly shaded at the middle and apex. The median spots of the upper surface reappear underneath in the shape of small black-ringed ocelli; the marginal spots and a few patches in the median and basal areas slightly silvered. ♀ rather paler than ♂, with the black markings heavier and the greenish-black shading more extensive. Under surface as in ♂, but the gaudy markings of the hind-wings even more pronounced, the greenish bands and spots contrasting more sharply with the darker ground. Expanse: 1·2″."

Genitalia:—Pl. 15, figs. 61, 62; pl. 16, fig. 64. As in the subsp. *nikolajewski*, there is a strong curvature of the ventral line of the head of the harpe, though otherwise the genitalia are typical of *B. napaea.* The curvature is not identical in the two specimens which were examined, but as it was present in both, as well as in the Asiatic subspecies which most nearly resembles subsp. *nearctica*, it strongly suggests that this development of the harpe head is a subspecific character among the eastern races of the species.

Identification:—The chief characteristic of subsp. *nearctica* is the beautiful coloration of the underside. Lehmann's description gives a good idea of this, but it appears to be more variable than he suggests, for in the three males that I have seen the predominant colour on the underside of the hind-wings was a pale yellow, through which the darker yellow-brown tone of the ground-colour appears here and there, but much less clearly than pl. 34, fig. 189 suggests. The female shows still more marked colour contrasts than the male, on the underside the ground-colour being a darker, redder tone, but the extreme, pale ochre of the upperside is almost more remarkable. The antemarginal area on the hind-wings is a deeper orange than the other parts, which gives the upperside an unusually variegated appearance. This is even noticeable in the photograph (pl. 34, fig. 190); the antemarginal area of the hind-wings shows much darker than the pale ochre margin (on the fore-wings), yet not so dark as the black basal suffusion. The pale ochre colour is a shade that as a rule only appears in aberrations of other races or species. Klots (1940), in differentiating his subsp. *halli* (the female of which on the upperside must be somewhat similar to the female of subsp. *nearctica*), states that both sexes lack the contrast and variegation of the markings on the underside, which is such a feature of subsp. *nearctica.* The underside should therefore distinguish the latter from subsp. *halli*, and the upperside from subsp. *alaskensis*, for Klots (*loc. cit.*) states that the female of the latter is much duller and exhibits less contrast on the upperside. Subsp. *nearctica* has really very little in common with subsp. *alaskensis*, with which it has previously been united; the black markings are heavier on the upperside, and the coloration of the underside is completely different. Elwes (1903), writing of the Arctic insects collected by D. Hanbury, and now in the British Museum, makes the statement when referring to subsp. *nearctica* (under the name of *B. pales*) that "the males are quite typical, and could not be distinguished from some Alpine specimens": I have never seen any European males of anything like a similar coloration on the underside, and even the upperside markings cannot be said to be quite typical of *B. pales* subsp. *pales*, being decidedly heavier than usual. Elwes continues: "The female is like some I have from Northern Siberia." These females, four in number, are now in the British Museum. They appear to belong to a large race (as yet undescribed) close to the subsp. *altaica* but much more heavily marked on the upperside, and more vividly coloured on the underside, where the ground-colour of the hind-wings is exceptionally dark. There are no males, so it is not possible to determine the systematic position of these specimens at present. There is a likeness in the brilliant and contrasting colours of the underside to some females of subsp. *palinoides* (compare pl. 40, fig. 251), but these show more of the dark ground-colour as a rule, and of course the colour of the upperside in subsp. *palinoides* is totally different.

Distribution :—A polar insect, replacing subsp. *alaskensis* north of the Arctic Circle. How far it ranges from east to west in the North-West Territories and Alaska is not yet known. Lehmann's specimens were taken at 69° 40′ N. Lat. and 141° W. Long. Mr. A. B. Klots informs me (*in litt.*) that he has seen only one specimen, a male, and it came from Barter Island, off the north coast of Alaska, which lies in 70° 15′ N. Lat. and 144° 0′ W. Long., and is at once the most northerly and westerly locality I know. To the east, a female in the Canadian National collection, taken by F. Johansen at Bernard Harbour, and the small series of three males and one female in the British Museum from 67° 40′ N. Lat. and 114° 30′ W. Long. constitute the most easterly and southerly localities. It seems probable the race will be found in many localities between these easterly and westerly limits, and perhaps beyond them. There is less likelihood of its extending much farther to the south. The specimen in the Canadian National collection, from Bernard Harbour, I assume to belong to this subspecies for the following reasons. The locality is much farther north than any others from which the subsp. *alaskensis* has so far been recorded ; but it would be quite normal for subsp. *nearctica.* The specimen was taken by F. Johansen of the Canadian Arctic Expedition, 1913, who was with the Southern Party, and we are told by Gibson (1920) that the localities visited by that party were in some instances the same as those at which the collections of D. Hanbury were made. Among the specimens taken by the latter were the series of subsp. *nearctica* now in the British Museum, labelled " 114° 30′ W. longitude, 67° 40′ N. latitude " (some of them are figured on pl. 34), a locality that must lie close to the coast of the North-West Territories just south of Wollaston Land in Victoria Island. There is every probability, then, that Johansen's female came from the same district, and even if it did not, it cannot have been separated from it by any great distance. In view of this, and the latitude, it seems impossible that it is a specimen of subsp. *alaskensis.*

(5) *B. napaea alaskensis* (Holl.).

Brenthis pales Schiffermüller, var. *alaskensis* Holland, 1900, *Ent. News* **11 :** 383.

Original description :—" Unfortunately, the collection contains only a single specimen of this interesting form. It differs widely upon the upper surface from specimens of *B. pales* coming from various European localities and contained in my collection. It comes nearer in general aspect to the variety named *generator* by Staudinger, coming from the Pamir and Transalai regions of Asia, but is smaller. The fuscous area of the basal portions of the primaries and secondaries is reduced, extending outwardly only to the middle of the cell, and the entire wing beyond this is bright reddish fulvous, with the characteristic lines and spots narrow and fine. The underside is marked much as in typical *pales.*

" Expanse 33 mm.

" 1 ♂, mountains between Forty-Mile and Mission Creeks, July 20 (Young)."

Genitalia :—Unknown.

Identification :—I have no first-hand knowledge of this race; and the description tells us nothing of the female. The admirable figure given by Gibson (1920 : pl. V, fig. 5) is helpful, but, unfortunately, he did not figure the female. The principal characteristics of the male are the bright ground-colour of the upperside and the fine black markings, tending to obsolescence, especially at the apex and outer margins of the fore-wings. In these respects the male of subsp. *alaskensis* is very similar to subsp. *nikolajewski*; it is, however, very markedly smaller. Holland states that the underside is much as in "typical *pales*," from which one can assume that it lacks any particularly bright or contrasting coloration. Gibson apparently shared this view, as he did not think it necessary to figure the underside. (It is perhaps as well to mention here, though the fact is probably well known, that the figure cited as "*alaskensis* Holl." by Lehmann (1913 : pl. 87, row e) shows a specimen of *Clossiana frigga* f. *alaskensis* Lehm.; there is no figure of *Boloria napaea alaskensis* Holl.). Of the female all I can say is that according to Klots (1940) it is much duller, more normally coloured, than the female of subsp. *nearctica.*

In spite of the fact that I have not been able to dissect specimens of this race and the following, I have no real doubt that they are correctly classified under *B. napaea.* The close similarity between subsp. *alaskensis* and subsp. *nikolajewski*, and between subsp. *halli* Klots and subsp. *nearctica*, makes it unlikely in the extreme that they would prove on dissection to be races of *B. pales.* I think it is safe to assume *B. pales* is wanting in N. America.

Distribution :—The geographical range of subsp. *alaskensis* is only very partially known; but it is by no means confined to Alaska. Holland's type came from east central Alaska, south of 65° N. Lat. Gibson (1920) states that there are three specimens in the Canadian National collection : two males taken 25 July 1912, at Racquet Creek, International Boundary, at 65° 20′ N. Lat. by D. D. Cairnes; and one male taken 5 July 1900 from the west branch of the Thelon river, MacKenzie, by J. Tyrrell. As one of the western branches of the Thelon connects with lake Tyrrell, one may suppose that this lake bears the name of the captor of the specimen, and that this is the branch of the river from which the specimen came; the locality must therefore have been a little north of the 63rd parallel. Finally, Mr. A. B. Klots informs me (*in litt.*) that in the American Museum of Natural History there is a series, mostly from Mt. McKinley, National Park. The large majority of known specimens therefore comef rom central and east-central Alaska at, and south of, the 65th parallel. The one exception is the specimen from MacKenzie, which, though a long way to the east of the other localities, is in about the same zone of latitude. It is certain that, with time, the insect will be found in many more localities between the eastern and western limits at present known.

(6) *B. napaea halli* Klots.

Boloria pales halli Klots, 1940, *Amer. Mus. Nov.* **1054** : 1–6.

Original description :—" Male.—Average length of fore-wing, 18·3 mm.

" Ground-color of upper side of wings bright orange-brown, very lightly tinged with pinkish or reddish. The usual transverse rows of spots and irregular lines are all present. Those in the basal half (or slightly more than half) of the wings are somewhat narrower than in most of the Palaearctic forms of the species, as is also the case with *B. pales alaskensis* (Holland). The fore-wings are dusted with fuscous scaling at the bases, somewhat more broadly along the inner margin than along the costa. The hind-wings are more heavily shaded basally than the fore-wings; but this shading almost always fails to reach the end of the discal cell.

" Ground-color of under side of fore-wing somewhat duller, and with a slightly more pinkish tinge than that of the upper side. The spots and bands of the upper side "show through " very faintly, those in and at the end of the discal cell more strongly. The apex and a narrowing border that does not reach the anal angle are yellow, slightly tinged with greenish. In this yellow area some of the spots of the upper side are repeated, of a brownish-red color; but these are of much smaller extent than the corresponding spots on the upper side.

" Ground-color of under side of hind-wing yellow slightly tinged with greenish; dark markings brownish red to bright red. In the great majority of the specimens the dark markings are so considerably diluted by dusting of the greenish-yellow ground-color that the entire wing shows a noticeable lack of contrast between the light and dark areas. With the exception of the large spot at the end of the cell, all of the markings, which in other subspecies of *pales* (especially most of the Palaearctic ones) are bright silvery white, here show only faint traces of a pearly luster, if any. The spot at the end of the cell is consistently white in color and only faintly pearly, never silvery, being thus less lustrous than in any of the other Nearctic subspecies and most of the Palaearctic ones. Especially noteworthy is the considerable reduction of the submarginal row of red, triangular spots which in other subspecies form the inner borders of the marginal row of silvery spots. In *halli* most of these red spots are reduced in size; this, in conjunction with the above-mentioned almost total absence of white, pearly or silvery, results in a very characteristic obliteration of the marginal row of spots.

" The males show comparatively little variation in color and markings, far less than would be expected in a species occupying a habitat that is subject to such extreme climatic changes.

" Female.—Average length of fore-wing, 19·02 mm.

" Ground-color of most of the area of upper side of both wings light gray, tinted with light brownish yellow. The color tends to be noticeably lighter, brighter and more yellow in the costal, subcostal and apical light areas and spots of the fore-wing, and in the anal light spots of the hind-wing. In sharp contrast to the general ground-color, the costal and subapical region of the hind-wing has the ground-color bright orange-brown, as bright as the ground-color of the male. Dark markings much heavier and more suffused than in the male.

" Ground-color of under side of fore-wing a somewhat darker, more reddish brown than in the male. The black markings of the upper side are nearly all repeated here, though much smaller than on upper side. The apical and outer-marginal light area is of a definitely more greenish yellow than in the male. The dark red markings in this area are as in the male. The black dots at the end of the veins are heavier than in the male.

" Ground-color of under side of hind-wing a more greenish yellow than in the male, the greenish tinge being more pronounced in the areas which on the upper side of the wing are black or fuscous. The dark red markings average only very slightly heavier than in the male; but since their hue is in greater contrast with the ground-color, the wing has a more contrasty and variegated appearance. As in the male the pearly or silvery white markings are all very much reduced in size and luster.

" There is a great deal of variation in the extent of the black markings and fuscous dusting on the upper side of the wings of the females, proportionately more than in the males. There is also considerable variation in the intensity of the dark red markings of the under side of the hind-wings."

" Types :—Holotype male, allotype female, 139 male paratypes and 57 female paratypes, all from the vicinity of Green River Pass, Wind River Range, Sublette Co., Wyoming, 18–31 July, 1939, taken by Klots and D. Bigelow. The holotype, allotype and a series of paratypes are in the American Museum of Natural History."

I have no knowledge of this newly-described race, and though I had hoped to obtain material for dissection which would have enabled me to describe the genitalia in this work, it has not been possible to do so. With his description Klots gave a very useful and detailed comparison between subsp. *halli* and the other American *Boloria* races; those interested in these insects should refer to his work.

Distribution :—The subsp. *halli* is said to be very abundant in the Hudsonian Life Zone meadows, at and above the timberline, which is at an altitude of 10,000–10,500 feet. The males were everywhere, visiting the flowers of *Arnica, Erigeron, Polygonum* and *Eriogonum*, which shows their tastes and habits to be similar to those of the European races; the females were much less numerous. Klots states (*loc. cit.*) that the insect was found everywhere they collected in the Hudsonian Zone, *i.e.* " in Stroud Creek Canyon, around Peak Lake, along the upper reaches of Trail Creek, around Summit Lake and the Elbow Lakes, in the upper parts of Pine Creek Canyon, and all along the trail from Summit Lake to Palmer Lake." The females were less often observed visiting flowers than the males, but were frequently seen resting in low willows, the latter being said to " form dense mats in the Hudsonian Zone bog areas." The race appears, therefore, to frequent both wet and dry areas, as do the *Boloria* races in Europe; but the vertical range of subsp. *halli* would seem to be considerably less than that of subsp. *napaea*, for Klots states that it is rare above 11,000 feet, from which one gathers that the vertical range may cover, at the most, some 1500 feet, just about half that of subsp. *napaea* in the European Alps.

(7) *B. napaea reiffi* Rs.

Boloria reiffi Reuss, 1925, *Int. ent. Z. Guben* **19** : 280.

No material of this insect is available. It was described from a single male from British Columbia. The locality suggests that it might be a slightly abnormal specimen of subsp. *alaskensis*, and Klots, who has seen another male from Atlin, B.C., which more or less agrees with Reuss's description, remarks (1940) that he suspects " *reiffi* will eventually prove to be a synonym of *alaskensis*."

Original description :—" Wie so viele Falter der nordamerikanischen Felsengebirge, deren nächste Verwandte circumpolare Verbreitung besitzen, mutet das vorliegende Tier wie ein Hybrid aus mehreren bekannten Arten an. Die Grösse und kräftige Zeichnung erinnert an norddeutsche *arsilache*, aber die Färbung der Hinterflügel-Unterseite, mit stark vortretender, gelber Grundfarbe, erinnert an die Unterseite vom ♀ *palina* Fruhst. aus Tibet, sogar an die noch gelbere Unterseite des *palinoides* m., nov. sp. (Vgl. Iris, Dresden, nächste Nr.), ♀, aus Szetschwan, China. Von dem Gelb heben sich, scharf abgegrenzt, die bekannten roten Binden und Flecke ab—die Unterseite wird hierdurch kontrastreicher als bei allen verwandten Arten. Silberzeichnung kräftig, normal verteilt.

" Nur ein Exemplar aus Britisch-Columbien, die Type ♂, in Koll. m."

2. *Boloria pales* ([Denis and Schiff.]).

Synonymy :—*Papilio pales* [Denis and Schiffermüller], 1775, *Schmett. Wien* : 177; *Papilio arsilache* Esper, 1780, *Die Schmett.* (1) **2** : Forts. 35, pl. 56, fig. 4 ♂.

Composition of species :—The species includes at least fifteen subspecies, for the greater part distinctly characterised, and spread over Europe and Asia. Only the position of subsp. *lucida* remains uncertain, as I have not been able to get specimens for dissection, but if, as I think likely, it proves to belong to

B. pales, it would be a sixteenth race. Only three local forms have so far been recognised, two of which are connected with the typical subspecies. When all the Asiatic races come to be as well known as the typical one, it is highly probable that more local forms will be found to exist; but one must remember that, as I have shown (1937), in the growth of a species the period of the greatest development of local forms precedes the period of greatest numbers of subspecies; so that in a species like *B. pales* where the number of subspecies is already high, the proportion of local forms is not at all likely to be great. On the other hand, I also demonstrated (*loc. cit.*) that the period of the greatest number of subspecies in the specific group coincides with great variability, both structural and superficial; and this is exactly what we find in the races that compose the *pales*-group.

(1) *B. pales pales* ([Denis and Schiff.]).

Pl. 34, figs. 192–197; pl. 35, figs. 198–207; pl. 36, figs. 208–217; pl. 45, figs. 306, 307.

Original description :—" Fam. K. . . . mit Silbermackeln."
(No.) " 8. Unbek. R.—Oraniengelber, unten roth- und silberfleckichter F.—*P. Pales*."

This description might equally well have implied *Clossiana euphrosyne*, but as the larva and food-plant of that species seem to have been known at the time of publication of the name, while those of *B. pales* were not, the reference to this point in the description was probably sufficient to establish the identity of the insect to which the name was applied.

Genitalia :—Pl. 17, figs. 71, 73, 75; pl. 19, figs. 81–86; pl. 20, figs. 87–92; pl. 21, figs. 93–96. The genitalia (see parts II, III and IV) are smaller and of markedly lighter build than these structures in the *B. napaea* races. This is most readily observable in the phallic organs. The average range of spinal development on the head of the harpe is equal to two-fifths of the total length of that structure. It will often be found helpful in comparing mounts of *B. pales* and *B. napaea* to contrast the proportions of the saccus. The difference in size can usually be recognised at a glance, even under quite low magnification.

Identification :—The characteristic features of subsp. *pales* have already been described in detail in connection with the identification of *B. napaea* (q.v.). It may be briefly repeated that the typical subsp. *pales* is best distinguished from *B. napaea* subsp. *napaea* by its slightly smaller size; more angular shape of the wings; heavier and more angular black markings on the upperside; the position of the second black spot of the median row on the fore-wings, touching (or almost so) the discoidal cell, especially at the upper end; the flattened external edges of the spots of the submarginal row, fore-wings; the ground-colour of the underside of the hind-wings, red-brown shades mixed with purple, the pattern very sharply defined and coloration bright; female monomorphic.

Apart from the typical subspecies of *B. napaea*, the only other *Boloria* race with which subsp. *pales* is known to fly is subsp. *balcanica*, of *B. graeca*; there is also a possibility that it may occur with the subsp. *brogotarus* of the latter, but this has not as yet been proved. Details of the identification of the *B. graeca* races will be given in connection with the latter.

Habitat and Period of Flight :—There is much variance in published records as to the vertical range of the typical subspecies of *B. pales* and *B. napaea*; no doubt the result of uncertainty in identification. Osthelder (1925) states the *B. napaea* on the average flies somewhat higher than *B. pales*; English authors, however, most usually state the reverse. Kitt (1912) records "*pales*" flying from 4500 to 7600 feet, in the Oetztal Alps, and from his references to the females it is clear he was including both species. Vorbrodt, who distinguishes them accurately, states (1928) that in the Zermatt district *B. napaea* flies between 5800 and 7500 feet, and *B. pales* between 6500 and 9750 feet (approximately), but adds that the latter ascends to over 10,000 feet on the Gornergrat. This would seem to settle the question that *B. pales* can establish itself at greater altitudes than *B. napaea*; but in some ways the Zermatt district is exceptional. It is well known that many species attain higher levels there than elsewhere in the Alps; also, that as *B. pales* ascends it loses size, and dwarf specimens (ab. *minor* Wehrli) of which the fore-wing is said to measure only 13 mm. in length, have been taken on the Theodul Pass at about 10,800 feet. It is therefore doubtful whether the species can be really at home at altitudes over 8000 feet, at which level normal-sized specimens still occur. It will also be noted that in Vorbrodt's records he says *B. pales* does not descend below 6500 feet in the Zermatt district, a level which is certainly abnormally high. In the Bernese Alps *B. pales* occurs on the Niesen from about 6000 to 7500 feet, while at Kandersteg I have myself taken it as low as just under 4000 feet. This is probably unusual; neither at this low level nor at levels much above 8000 feet will the insect occur in any number, as it does between 5500 and 7500 feet. For this reason I accept this zone as the normal habitat of subsp. *pales*. This, of course, corresponds with the range in altitude of *B. napaea*, and my own experience has been that as one approaches the 8000-foot level the colonies of both species become numerically less. It also so happens that whenever above 7500 feet I have come on either species, the other has also been found after further search. It seems one would be correct in saying that, though *B. pales* certainly can maintain itself at altitudes of one, or even two thousand feet, above those frequented by *B. napaea*, it can only do so at the expense of its vitality, the colonies losing numbers, and the individuals size. As to the nature of the ground most frequented by *B. pales*, it seems to occur almost universally within the normal zone of altitude. Dry or swampy ground, flat valley stretches or steep hill-sides, grassy alps or rocky inclines, all seem to afford the species everything it needs. It is fond of settling on flower heads; Vorbrodt mentions (1928) that in dull or cloudy weather it is especially fond of resting on heads of *Arnica montana*, an observation which applies equally to *B. napaea*. In bright sunshine, too, they can often be seen in numbers on the *A. montana* heads, with their wings spread wide open.

The flight period varies according to the altitude. Vorbrodt (*loc. cit.*) gives it as from 14 June to 20 September. These, presumably, are the earliest and latest dates he obtained, and do not imply the length of the flight period in one locality. So far as I can gather, this would be between four and five weeks.

Subsp. *pales* f. *palustris* (Frhst.). Pl. 37, figs. 218–221; genitalia pl. 21, figs. 97, 98.

Argynnis pales palustris Fruhstorfer, 1909, *Int. ent. Z.* **3** : 112.

Original description :—"Wheeler, Rühl, Seitz erwähnen bereits eine der *arsilache* benachbarte kleine Form der alpinen *pales*, die in den südschweizer Gebirgen anfängt aufzutreten, wo die grössere als typisch aufgefasste *pales*-Form ihre Höhengrenze erreicht oder sich wie im Engadin an Seeufern oder auf Mooswiesen wie bei Arolla einfindet.

"*Palustris* differiert von *arsilache* aus Königsberg, dem Harz und *pales pales* aus den österreichischen Alpen durch ihre Kleinheit und die manchmal dunkler rote, aber stets kleiner weiss punktierte Unterseite.

"♀ bleicher als norddeutsche und österreichische Exemplare.

"Simplon-Culm, Zermatt, Arolla, Engadin; Cognetal, Piemont, Champery."

This name has been used in a very haphazard manner. Vorbrodt (1928) tried to restrict it to those small aberrations, with dark red underside, which most often occur in swampy localities at great altitudes. He tried to support this use of the name by taking certain points from Fruhstorfer's description, rather at random, and ignoring the rest of it, Other writers have applied it in a general way to any forms of subsp. *pales* which are not quite typical; but mostly they have taken it as a subspecies, which is impossible, for it never (according to the material I have seen) occurs as a pure race, *i.e.* independent of typical subsp. *pales.* Fruhstorfer seems to have intended the name to apply to abnormally small specimens from high altitudes; but the localities he gives indicate a form of much wider distribution. He distinguishes between *palustris* and the subsp. *alethea* from north Germany and the Harz Mountains (*i.e.* what he calls *arsilache*), and typical subsp. *pales* from Austria, noting *palustris* as smaller, and *sometimes* (italics mine) with a dark red underside, but with reduced white (*i.e.* silver) spotting. Finally he adds that the female *palustris* is paler. He complicates matters by including a small race that occurs "on the borders of mountain lakes in the Engadine," which actually is subsp. *aquilonaris*, but it is clear he did not realise the identity of the latter, especially as it does not occur in any of the other localities he gives, so it can be disregarded. Even if it was intentional on his part, the previous existence of the name would have restricted his *palustris* to the forms of the other localities he mentions, for they belong to a different subspecies.

We have, therefore, the following characters to distinguish f. *palustris* from subsp. *pales.* It is smaller, the underside sometimes darker red, the silver spots smaller or reduced in number, female paler upper and underside. These characters apply to a small proportion of individuals of subsp. *pales* in the central Alps, but they mostly occur with considerable numbers of other atypical forms, usually much duller and less sharply marked than either typical subsp. *pales* or f. *palustris* as suggested by Fruhstorfer's description. Such fluctuating forms, which are united to both the typical subspecies and the darkest and smallest f. *palustris* by imperceptible degrees, can only be included under the latter name, for there is no question that all are products of common lines of variation, inherent in subsp. *pales.* It is, therefore, in this broad sense that I use the name *palustris.* In some localities these variable individuals are so numerous that there might be ground for suggesting they constituted a genuine local race, excluding subsp. *pales*; but I doubt if this ever actually is the case. Further, subsp. *pales* occurs in very many zones in the eastern Alps, and here f. *palustris* is unknown. Also subsp. *pales* can occur as a pure race in the very centre of the *palustris*-zone, as for example on the Niesen in the Bernese Alps (see pl. 36, figs. 214–217), though within a few miles, in the Kandersteg district, f. *palustris* predominates.

One of the difficulties connected with the identification of f. *palustris* is of course its great variability. This to a considerable extent is connected with locality. I have dealt with this aspect of the variability of the insect already (see p. 39), so need not do so again here; but I may briefly recall the facts which are of most importance. As subsp. *pales* ascends, it loses size and is inclined to get darker in colour; consequently at high levels f. *palustris* is smaller and darker, at lower levels, larger and paler, and this is progressive throughout the entire vertical range of the subspecies. At the lowest levels the paler female and poorly marked male are even less like typical subsp. *pales* than the small, dark, high-level specimens. But there is a complete chain of intergrades between these extremes, and there is no question that all these varying individuals are but local products of the one racial strain, subsp. *pales*. As I have already pointed out, therefore, all individuals which deviate from the typical subspecies in size or coloration, in the central Alps and a little southwards, are referable to f. *palustris*. If it be objected that Fruhstorfer specified that his *palustris* was " small " and only replaced the larger race at high levels, I would point out that all this was quite uncertain; he was, most probably, including *B. napaea* in his conception of subsp. *pales*, which accounts for his emphasis on the small size, and there is no such thing as a race of fixed size at any level. He was careful to say " sometimes " in respect of the darker red colour of the underside, and there can be no doubt that the same qualification is necessary in all other respects also. On pl. 37, figs. 218–221 show some examples that coincide with Fruhstorfer's description very closely; but it will be noted that the underside of the male (fig. 219) has strong silvery spots, even if they are smaller than those in the fine specimens from the Allgauer Alps (pl. 35) or the Tatra and Carinthia (pl. 34). It is not possible to restrict the name " *palustris* " to these specimens, however, for variation is so general, that a series taken at Zinal in another season might have quite a different appearance, and these small specimens are connected to larger ones of very different appearance by such a variety of transitions, that it is impossible to maintain that they constitute two distinct races.

Distribution:—The subsp. *pales* appears confined to the central and southern Alps of Europe; it is very widely distributed within this area. The eastern limits of its range are uncertain. The Tatra is the most easterly locality from which I have seen specimens, or obtained authentic records. The race attains what is probably its finest development in these mountains (see pl. 34, figs. 192–195). Heyne (1895) states that the species occurs in the " mountains of Bucovina." I have not been able to get confirmation of this record, or find any others from the Carpathians in general. Farther south, it is not known in the Transylvanian Alps either. Diószeghy in his work on the Retyezat District (1930) does not mention it. To the west, Hoffmann and Klos (1914) state it is widely distributed in the mountains of north Styria; Höfner (1904) records it as abundant in the Glockner district of Carinthia, and I have come on it myself in two localities at the eastern end of the Hohe Tauern range. Farther north, subsp. *pales* is widely distributed in the Salzkammergut, the Salzburg Alps and the Bavarian Highlands, and from these districts one gets the first records in the eastern Alps of f. *palustris*, often under the name of "var. *deflavata* Wagner."[4]

Throughout the Tyrol, as far south as the Dolomites and Adamello Alps, subsp. *pales* is very generally distributed, but apparently without f. *palustris*. The latter occurs in numbers in the Ortler Alps, perhaps one of the most easterly localities, where it appears as a form rather than an aberration. On entering the Swiss Alps the proportion of f. *palustris* increases rapidly as one passes westward. In the Grisons it still appears as a recurring aberration, and pure colonies of subsp. *pales* are not uncommon. Throughout the Rhaetian and Bernese Alps f. *palustris* is found in most localities where subsp. *pales* occurs. A pure colony of the latter exists on the Niesen in the Bernese Alps, ranging from about 6000 to 7200 feet, and most probably other such colonies exist in this central district, and in the neighbouring Alps as far east as the Alps of Glarus. In the Pennine Alps f. *palustris* seems to occur everywhere, and usually constitutes a high proportion of every colony; it is even possible that in a few localities at extremely high levels, such as those recorded by Vorbrodt in the Zermatt district (at over 10,000 feet on the Gornergrat, and about 700 feet higher on the Theodul Pass), no typical subsp. *pales* may be taken during long periods. Such instances, however, cannot be taken as proof that f. *palustris* is a pure race in these localities, for there is evidence enough to show that it is only the abnormal conditions prevailing at these great altitudes that prevent the race developing properly. At any time, as the result of an abnormally mild season, examples of the parent subspecies might reappear. Passing south from Switzerland, typical subsp. *pales* remains scarce in the Savoy Alps, and f. *palustris* frequent. A change, however, is taking place in this district, which may probably be said to mark the true southern limit of the range of subsp. *pales* as such. Throughout the Cottian and Maritime Alps, and probably a large portion of the Graian Alps also, it is replaced by another form, and in this area specimens of the parent subspecies only occur sporadically.

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[4] This is an incorrect use of the name (*Argynnis pales* Schiff. ab. et var., *deflavata* Wagner, 1909, *Ent. Z.* **23**: 17; " Dachsteingebiet:—Ochsenwiesalm, Kogelgasse ") which only applies to aberrations in which all yellow coloration on the underside is lost. Such specimens occur anywhere among subsp. *pales* or f. *palustris*, but as a varying amount of yellow coloration is a normal characteristic of the latter form, it is impossible to use " *deflavata* " in place of " *palustris*." It may be noted that even at extreme altitudes, where the red coloration most frequently tends to spread over the underside of the hindwings, it is only in a limited number of individuals that all the yellow is obliterated.

Although subsp. *pales* does not leave the main chain of the Alps in the west, in the extreme east it breaks away and extends to the Tatra; in the south-east also it has spread a considerable distance, and is known in a few localities in the Balkans. Drenowski (1925) recorded only subsp. *pales* from the Rilo Mountains, at 1600 m.; Haig Thomas (1936) took it on the Belmeken at 7200 feet, in the Rhodope Mountains. Elwes found it in the Rilo at 5000 feet, on the same ground as *B. graeca* subsp. *balcanica*, and at the same date; the specimen figured on pl. 45 (figs. 306, 307) was one taken by him, as were the specimens of *B. graeca* subsp. *balcanica* shown on pl. 46 (figs. 308–311). In his article dealing with these insects (1900) he makes no reference to typical subsp. *pales*, which he evidently did not recognise; this probably is the reason why he asserts that *B. graeca* subsp. *balcanica* is transitional between subsp. *pales* and subsp. *caucasica*.

Dr. L. G. Higgins informs me (*in litt.*) that, farther to the north, he has taken subsp. *pales* above lake Bled in Yugoslavia. Although subsp. *pales* is much more localised in the central and south-central Balkan mountains than *B. graeca*, according to Drenowski it is often abundant where it occurs. It may yet be discovered in other localities in this region.

Subsp. **pales** f. **mixta** form. n.

This remarkable southern form is in some degree transitional between subsp. *pales* and subsp. *pyrenesmiscens*. In general appearance it resembles both in some respects, yet obviously is not referable to either. It is characterised by the range of variability of the coloration of the underside, the extremes of which are so marked that if they were more constant they could be said to constitute two distinct types of coloration. In most localities, however, they merge completely; and this intermediate type shows the normal aspect of the form. This colour-variability only affects the underside; in one extreme the hindwings are pale, with the yellow tone predominating and the red-brown areas also pale; in the other the red-brown predominates, and sometimes is so dark that many individuals closely resemble the parent subsp. *pales,* occasional examples being indistinguishable from it. For this reason f. *mixta* cannot be classified as a true subspecies. The markings of the underside are, however, different in character from those of subsp. *pales,* being less sharply defined. The general effect is to produce a washy look, as though the pattern was being obliterated; this is seen in both sexes, but the females are paler than the males. The upperside is always a pale, dull, yellowish-orange, paler than the colour of subsp. *pales* but not quite as pale as that of subsp. *pyrenesmiscens.* On the underside the markings are suggestive of the latter, but less sharp, and never show the greenish tinge in either sex. Considering the variable nature of the coloration of the underside, it is not surprising that small numbers of f. *mixta,* from various localities, have been referred to by some writers as "*pales,*" "*palustris*" and "*graeca*"; f. *mixta,* however, never develops the characteristic markings of these, and it will only be at the highest levels that small specimens, which might be referable to f. *palustris,* will be found. Unfortunately, material was not available in time for illustration in this work, or to enable me to study the genitalia in detail.

Distribution:—This form is widely distributed throughout the Cottian and Maritime Alps, it also extends north into the Graian Alps, though how far is unknown. The holotype and paratypes came from Briançon in the Cottian Alps; they are in the British Museum (Nat. Hist.).

(2) *B. pales caucasica* (Lederer).

Pl. 37, figs. 222–225.

Synonymy:—*Argynnis pales* Schiff. var. *caucasica* Lederer, 1852, *Verh. zool.-bot. Ver. Wien* **2**: 22; nom. nov. pro *Papilio arsilache* Esper, Herrich-Schäffer *nec* Esper (1845), *Syst. Bearb. Schmett. Europ.* **1**: pl. *Pap.* 55, figs. 259, 260 (males), 261, 262 (females).

Original description:—Lederer's name was based on Herrich-Schäffer's figures; the latter gave the locality for the insects figured as "Kaukasus" (Herrich-Schäffer, 1845, *ibid.* **1**: 163).

Genitalia:—Pl. 22, fig. 99. There is nothing particular to note about the structure of the male armature of this race. Although, superficially, it forms a transition between subsp. *pales* and those races that centre round the subsp. *sipora,* anatomically there is no indication of this fact. There is, however, some suggestion of affinity with subsp. *pyrenesmiscens* in the formation of the head of the harpe, though of course this type of formation is not confined to these two subspecies. At the most it can be said to be of more frequent occurrence in subsp. *pyrenesmiscens* than in any other race, but, on the other hand, variation of the head is characteristic of *pyrenesmiscens.*

Identification:—The subsp. *caucasica* is the first of those races (all Asiatic) in which the ground-colour on the upperside is more completely uniform in shade all over, and dull in tone, though without loss of intensity. In actual tone the colour of subsp. *caucasica* is nearest to that of the subsp. *baralacha*; but the ground-colour of the underside is more yellow-brown in the male (more orange or red-brown in subsp. *baralacha*) and a paler tone in the female. The black spotting of both upper and underside is stronger than in subsp. *sipora,* and, of course, markedly more so than in subsp. *baralacha.* The extent and position of the black spotting of upper and underside is suggestive of the subsp. *pyrenesmiscens,* as are the markings of the underside of the hind-wings. Subsp.

caucasica, however, differs very markedly in the rounder shape of the black spots, and the beautiful golden colour of the central band on the underside of the hind-wings. This feature, to a certain extent, gives the race a likeness to the f. *mixta* of subsp. *pales*, but the character of the black spotting of both upper and underside in subsp. *caucasica* is totally different, for, as already noted, all the spots tend to be rounded (even those of the median row on the upperside of the fore-wing) and not linear as in subsp. *pales* and all its forms. Also, on the underside of the fore-wings in subsp. *caucasica*, the black spots are strongly developed, and this immediately distinguishes it from form *mixta*, in which the underside of the fore-wings is almost completely without black spots, while the few which occasionally do appear are distinctly linear and not rounded.

On the whole the subsp. *caucasica* probably most resembles subsp. *sipora*, from which it principally differs in the golden colour of the underside of the hind-wings, in contradistinction to the more red-brown tone in the latter, and in the heavier black spotting on the upperside of all the wings, and the underside of the fore-wings.

Distribution :—So far as is known, subsp. *caucasica* is confined to the Caucasus.

(3) *B. pales sipora* (Moore).

Pl. 37, figs. 226, 227; pl. 38, figs. 228, 229.

Argynnis sipora Moore [1875], *Proc. zool. Soc. Lond.* **1874** : 568, pl. 66, fig. 11.

Original description :—" Upperside pale fulvous in the male, dusky fulvous in the female.

" *Male*—fore-wing with black narrow short streak, two small spots, and a recurved streak within the cell, a curved streak at its end, a dentate spot beneath and an irregular transverse discal series of lunules beyond the cell; a transverse discal row of conical spots, a submarginal row of triangular spots, and a marginal line formed into less-defined spots, one being at the end of each vein: hind-wing with two narrow streaks at end of the cell, a transverse discal series beyond, two outer and a marginal row of spots. *Female*—black markings broader, the submarginal row of spots on both wings large and with pale whitish outer marginal border: cilia white.

" Underside, *Male*—fore-wing paler, markings indistinct, apex and exterior border yellow, streaked with red: hind-wing yellow, abdominal margin greenish, a broad irregular subbasal and discal transverse red band, the basal band enclosing a pearly-white round spot within the cell and an elongated spot beneath it, the band bordered exteriorly by three pearly-white transverse streaks; within the discal band the upper and lower portions are slightly streaked with pearly-white, and on the middle portion is a series of five blackish spots; on the outer margin of the wing is a row of quadrate pearly-white spots. *Female*—fore-wing dark fulvous; markings more prominent, apex and margin greenish: hind-wing with the base and middle portion dark green, the subbasal and discal bands dark chestnut-red; markings as in the male.

" Exp. ♂ $1\frac{3}{8}$, ♀ $1\frac{4}{8}$ inch. *Hab.* Cashmere, near Gungabul lake, at foot of Haramook Peak (Capt. H. B. Hellard)."

Genitalia :—Pl. 18, fig. 80; pl. 22, figs. 100, 103. In this, and the two following subspecies, there is a tendency to develop a subspecific character in the formation of the clasper. This is slightly more curved ventrally, and deeper in proportion to its length, than is usual. That these features are only subspecific developments is shown by the complete absence of constancy in both. The ventral curvature also appears in subsp. *pales* at times, though never attaining in that subspecies quite the extreme which is attained in subspp.

sipora and *baralacha*. The variability in the shape of the head of the harpe is no less than in the other subspecies (compare pl. 18, fig. 80, and pl. 22, fig. 100).

Identification:—Very similar to subsp. *baralacha*, from which it has been said to be indistinguishable by some authors. It is, however, a more heavily marked insect, all markings, both upper and underside, being sharper and darker. The development of the black spots, not only on the upperside of the hind-wings, but also on the underside of the fore, is decidedly stronger, even in the females (compare pl. 38, fig. 229 with fig. 237). On the underside of the hind-wings the ground-colour is more or less similar in both, but the central band is yellow with a suffusion of orange, which turns to greenish near the inner margin. In subsp. *baralacha* the central band is a beautiful clear, golden-yellow, and all the silvery spots are stronger than in subsp. *sipora*. It may be possible that poorly-marked aberrations of subsp. *sipora* would be difficult to identify, but if other specimens from the same locality were available, it should be obvious that the troublesome specimen was abnormal.

Distribution:—It is impossible, in the case of the Asiatic races, to form any real idea of their geographical range. This must be left for future workers to discover. Subsp. *sipora* is, apparently, widely distributed in Kashmir, ranging from the Burzil Pass in the north-east, to the Kulu District of the Punjab. It is found at great altitudes, ranging from 11,000 to 13,000 feet, according to the labels of such specimens as I have seen, but in all probability it occurs considerably higher than this. The period of flight seems to be mid-July to mid-August.

(4) **B. pales nitida** subsp. n.

Pl. 38, figs. 230–233.

This fine race is unquestionably very close to subsp. *sipora*, but it is constantly larger in both sexes, as can be seen by a glance at the figures on plates 37 and 38. As well as this increase in size, both male and female are much richer in coloration, the upperside being a decidedly redder tone than in either subspp. *sipora* or *baralacha*; and in the female the colour is quite uniform all over. The underside is very striking, especially in the male; the ground-colour of the hind-wings ranging from a beautiful deep venetian-red (in some specimens slightly pinker) to cinnamon. This colour often closely resembles the colour of the blossom of the beautiful *Potentilla nitida*, for which reason I have adopted this name for the race. The central band is a clear golden colour, contrasting very sharply with the ground-colour, and almost without the dark suffusion that so frequently obscures the band in other races; only quite near the inner margin does a slight greenish superscaling occur. This superscaling is stronger and more extensive in the female, and the ground-colour is paler, and much yellower in tone. The black spotting on the underside of the fore-wings is variable in both sexes, sometimes being markedly less than in the specimens figured.

Subsp. *nitida* is easily distinguished from subsp. *baralacha* by its much greater size, as well as the far heavier black spotting on the upperside and the characteristic coloration of the underside. The holotype and allotype, which are figured, and paratypes are in the British Museum.

Genitalia:—Pl. 22, fig. 101. The genitalia of subsp. *nitida* show that, as its superficial appearance suggests, it has close affinities with the subspp. *sipora* and *baralacha*, the same prominent curvature of the ventral line of the clasper, and its consequent increase in depth, being marked. There is also a tendency to a reduction in width of the wings of the phallobase, which, if developed to a slightly greater extent and constant, would suggest a specific distinction. This characteristic is most developed in subsp. *nitida*, and least in subsp. *baralacha*. The variable nature of all these structural features, however, is such that no question of these races being specifically distinct from the other *B. pales* races can arise at present.

Distribution :—So far as one can ascertain from the small series of specimens in the British Museum, subsp. *nitida* occurs only in the Baltistan district of Kashmir; the male holotype coming from Chogo Lungma, Baltistan, at 13,000 feet; the female allotype from the Stakspi Pass, at 12,000 feet; and paratypes from the Deosai Plains at 13,000 feet. All the specimens were taken in late July or early August.

(5) *B. pales baralacha* (Moore).

Pl. 38, figs. 234–237.

Synonymy :—Argynnis baralacha Moore, 1882, *Proc. zool. Soc. Lond.* **1882** : 242; pl. 11, fig. 1, 1a; *Argynnis pales hunzaica* Tytler, 1940, *J. Bombay nat. Hist. Soc.* **42** : 120.

Original description :—" Male upperside fulvous: lower basal area of both wings minutely black-speckled: fore-wing with a black recurved streak within the cell, a lunular streak at its end; a discal transverse zigzag series of broader streaks, two outer rows of small spots, which are indistinct at the apex, and a marginal, indistinct, dentated lunular speckled line: hind-wing with two less distinct and more slender cell-streaks, discal row of spots, two outer rows of spots (of which the inner row is indistinct), and marginal speckled line.

Underside—fore-wing paler fulvous, with the cell, discal and inner row of black spots as above showing very indistinctly; the costal border, two streaks from the apex, and short X-shaped marginal marks being yellow: hind-wing yellow, with a very irregular transverse subbasal, discal, and marginal fulvous-red band; the subbasal band bordered outwardly by linear pearly streaks, the discal band by indistinct pearly lunules, and the marginal band traversed by pearly X-shaped marks; the discal and marginal bands more or less confluent; a small pearly spot also within the cell.

" Expanse 1⅝ inch. Hab. Ladak."

Genitalia :—Pl. 22, fig. 102. As already noted, the development of the genitalia in this race is more or less similar to that of the last two races; but the wings of the phallobase are not, apparently, so liable to reduction in width, and in this respect show a closer affinity with the other *B. pales* races.

Identification :—Staudinger and others tried to sink subsp. *baralacha* as a synonym of subsp. *sipora*. Turner (1917) refers to it as a mutation of *sipora* not worth a distinctive name. Although there is a general resemblance between subsp. *baralacha* and subsp. *sipora*, the former is slightly smaller, the black markings much finer (less heavy) on the upperside, and on the underside of the fore-wings also, and the colour of the upperside is a duller orange. Although difficult to describe, this tone of colour is quite distinct when compared with that of subsp. *sipora*, and the reduced size of the black spots and markings on the upperside is also distinctive. The ground-colour of the underside of the hind-wings is similar to that of subsp. *sipora*, but the golden central band is clear, less suffused, more resembling that of subsp. *nitida*; from the latter, however, there is no difficulty in distinguishing subsp. *baralacha* owing to its smaller size and thin, black markings. The name *hunzaica* has recently been given to specimens from N.W. Kashmir, but the description of these shows them to be indistinguishable from subsp. *baralacha*. The description is as follows :—

" Male. *Upperside* with all markings on both wings much smaller and less pronounced than in *A. pales sipora* M. Underside of fore-wing with no spots on disc of wing; a subapical brown streak pointing to the dorsum; below this there is a submarginal row of five small black spots in 6–2, the spots in 2 and 3 being more inwardly placed. Hind-wing ground-colour more extensive and yellowish than in *A. pales sipora* M.; submarginal spots blackish red and conspicuous.

" The hind-wing of a different shape to *sipora* M., in *hunzaica* the termen is round; in *sipora* M., it is rather straight from the apex to vein 4, and then sharply bent inwards to the tornus, giving the rather square look."[2]

This description was taken from eight males and one female captured by native collectors in August; the locality given as " Mizgah, Hunza."

It will be noted that in this description no comparison is made with subsp. *baralacha*, so one can only suppose Tytler assumed it to be identical to subsp. *sipora*; also the size of *hunzaica* is not mentioned, so it may be taken as close to that of subsp. *sipora*. The features of the markings on the upperside and the underside of the fore-wings are those of subsp. *baralacha*. The reference to the ground-colour of the underside of the hind-wings shows that Tytler assumed the area I call the " central band " to display the ground-colour, and in this sense the features he mentions also show agreement between his specimens and subsp. *baralacha*. These points, in conjunction with the fact that Tytler was apparently unaware of the existence of, or at any rate the characteristics of, subsp. *baralacha*, suggest that he inadvertently redescribed it.

Distribution:—The subspecies was apparently known only from the Ladak district of Kashmir, until the discovery in the N.W. of that province of the specimens Tytler described. In the southern area it extends to Koksar in the eastern Punjab. The Bara Lacha Pass reaches an altitude of over 16,000 feet, but there is no means of telling what the highest level to which the insect ascends may be. The flight period, as in all races established at these great altitudes, is July and August.

(6) *B. pales eupales* (Frhst.).

Synonymy:—*Argynnis pales eupales* Fruhstorfer, 1903, *Soc. ent.* **18**: 124; *Argynnis pales eupales* Fruhstorfer, 1904, *Deuts. ent. Z.* " *Iris* " **16**: 307.

This is one of those cases in which Fruhstorfer's descriptions were published twice. The following description is from *Iris*.

Original description:—" Von *pales*, der sie merkwürdiger Weise näher steht als *pales generator* Stdgr. weicht *eupales* ♂ oberseits durch die viel breiteren, schwarzen Binden und Punkte und die dunklere Flügelbasis ab.

" Unterseite: Auf den Vorderflügeln sind die schwarzen Binden gleichfalls schärfer markiert und alle rotlichen Makeln sind dunkler braun.

" Die Hinterflügel sind bunter, die in *pales* gelbbraunen Binden und Flecken sind dunkel rotbraun und schmäler und viel mehr gezähnt, und eingekerbt.

" Diese Einkerbungen werden verursacht durch die reduzierteren, aber schärfer gebogenen Silberflecken.

" ♀. Das ♀ zeigt auf der Vorderflügel-Oberseite gleichfalls breitere Binden und der Apex trägt einen deutlich markierten hellgelben Fleck. Der Apicalteil der Vorderflügel-Unterseite ist breit hellgelb und wird von einer hellrotbraunen, kurzen Binde durchzogen. Der Marginalsaum trägt rotbraune Makeln.

" Hinterflügel-Unterseite: Diese ist vor allem ausgezeichnet durch eine schmale, scharf gezackte, fast ganz schwarze Discalbinde, welche eine hellsilberfarbene Region in der Mitte teilt. Der braune Subbasalfleck ist fast dreieckig und sendet eine scharfe Spitze in die

Flügelmitte. Die submarginalen und subanalen Punkte und Flecken sind tiefer braun und breiter ausgemalt als in *pales* ♀♀.

"Khamba-Jong, Süd-Tibet. 3 ♂♂, 5 ♀♀ in Coll. Fruhst."[5]

Genitalia :—Unknown. The genitalia in the three following subspecies, to which *eupales* is probably closely related, do not show any definable subspecific characteristics; individual variability is very frequent and often marked.

Identification :—The subsp. *eupales* is the first of a small group of eastern races that are characterised by the extremely variegated and rich coloration of the underside of the hind-wings, the pattern of which is also much more irregular, the edges of the bands and spots being much more jagged than in the western races of the species. The black markings on the upperside in subsp. *eupales* are apparently heavier in proportion to its size than in subspp. *palina* or *palinoides*; subsp. *eupales* is further distinguished from subsp. *palinoides* by the shape of the wings, which are longer and narrower, more as in subsp. *palina*. The ground-colour of the underside of the hind-wings is dark, the central band narrow, and (presumably) heavily suffused with dark scales, rendering it very obscure especially in the female; the marginal silvery spots are bright, though reduced. This coloration of the underside should distinguish subsp. *eupales* readily from subsp. *palina*, which on the whole it must otherwise most resemble.

Distribution :—Described from southern Tibet, where Seitz (1909) states it occurs at about 9000 feet. It is probable that it is a somewhat local race, for there are no specimens of it in the British Museum, although there are a certain number of the following race from various localities in Tibet.

(7) *B. pales palina* (Frhst.).

Pl. 39, figs. 238–247.

Argynnis pales palina Fruhstorfer, 1903, *Deuts. ent. Z.* "*Iris*" **16** : 306.

Original description :—"Steht *sifanica* Gr. Gr. sehr nahe, ist aber etwas grösser, von spitzerem Flügelschnitt und auf den Hinterflügeln länger behaart.

"Die Schwarzfleckung aller Flügel ist ausgedehnter, was sich besonders am Marginalsaum bemerkbar macht.

"Die schwarze Medianbinde aller Flügel ist mindestens doppelt so breit als bei *pales* typica und *sifanica*, aber weniger kräftig als bei *arsilache*.

"Unterseite: Verglichen mit *sifanica* sind ähnlich wie bei *eupales*, alle rotbraunen Flecken, Binden und Punkte stark verbreitert, namentlich die Basalflecken, und die Discalbinde ist stark prononciert. Die in *sifanica* vorhandenen, subanalen Silberpunkte der Hinterflügel sind ebenso wie bei *eupales* stark reduziert und fehlen häufig.

"Ta-Tsien-Lou, 2 ♂♂, Siao-Lou, 1 ♂, von Herrn Charles Oberthür im Tausch empfangen."[1]

Genitalia :—Pl. 22, fig. 104; pl. 23, figs. 105, 109, 110. The subsp. *palina* is the only one of the eastern races of the species (as far as my knowledge of these races at present goes) that develops in the genitalia a feature suggestive of the subsp. *aquilonaris*. In the latter the ventral edge of the head of the harpe is strongly concave; in subsp. *palina* this concavity reappears, though not quite so fully developed. In spite of this, it must be noted that the proportion of the total length of the harpe on which spines are developed is slightly greater in the subsps. *aquilonaris* and *alethea* than in the other *B. pales* races; in this respect, however, subsp. *palina* agrees with subsp. *pales.* As the ventral curvature of the head appears at times in all *B. pales* races and is not of specific constancy in subsp. *aquilonaris*, it is not to be assumed that this slight curvature indicates any close affinity between subsp. *palina* and the subspp. *aquilonaris* and *alethea.*

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[5] In Fruhstorfer's first description (*Soc. ent., loc. cit.*) the name of the locality was given as "Kham-Ha-Tong"; this, almost certainly, was a slip for "Khamba-Jong," which appears in most atlases, there being no reference to the former.

Identification :—Subsp. *palina* is said to resemble subsp. *eupales* more nearly than any other race, but differs from it both in size and in the colour and pattern of the underside. Subsp. *palina* is larger, and the black spots on the underside of the fore-wings in both sexes are said to be stronger; the ground-colour of the hind-wings is equally deep but redder (a deep venetian red), tending to include purple tones in the submarginal area; the central band is broad and densely powdered with red scales in the male, which gives it a very distinctive appearance; all the silver spots are very bright. The female is paler both upper and underside, and though usually the dull orange ground-colour of the upperside is light (as in pl. 39, fig. 244), very darkly suffused specimens also occur (as pl. 39, fig. 246). This, so far as I know, is the only race besides subsp. *generator* in which the female is dimorphic. On the underside the female shows great contrasts in colour, the central band and marginal lunules are yellow, all the silver spots are reduced, and wanting in some specimens; the central band is very broad and clear; the ground-colour a still darker shade of the same red as in the male. From subsp. *palinoides*, subsp. *palina* is distinguished by its larger size; longer shape of wings; the black spots on the upperside thinner, especially along the wing margins, causing the fringes to appear less clearly checkered. On the underside the black spots on the fore-wings are also weaker, and the dark ground-colour of the hind-wings more pronounced, especially between the central band and the wing margin, where the pale markings in subsp. *palina* are reduced, the prominent pale wedge between nervures 3 and 4, which in subsp. *palinoides* almost unites with the central band, being reduced to a marginal spot. This character is very marked in the male, but in one female (pl. 39, fig. 245) the pale wedge is present, nearly reaching the central band; it will be seen, however, that in this specimen the pale spot on the costa, near the apical angle, is quite normal in development, and does not spread so as almost to unite with the spot at the apical angle as in subsp. *palinoides* (see pl. 40, fig. 251).

Distribution :—Fruhstorfer's types came from Ta-tsien-lu and Siao-lu in Szechwan; but *palina* evidently has a wide range, for there are specimens in the British Museum (from the Oberthür collection) labelled " Frontière orientale du Thibet," and others from " Tusk," " Nyenyam " and " Hou-Kow," fairly widely separated localities in Tibet, and yet others from Sikkim taken at altitudes between 13,000 and 15,000 feet. The specimens from the Oberthür collection, figured on plate 39, are very probably topotypes; for it was from Oberthür that Fruhstorfer obtained the specimens he described.

(8) *B. pales palinoides* Reuss.

Pl. 40, figs. 248–251.

Boloria pales f. geogr. *palinoides* Reuss, 1925, *Deuts. ent. Z,* " *Iris* " **39** : 218; (*in* Draeseke).

Original description :—" Tat. In Anzahl Sump. Viel feuriger gefärbt als *palina* Fruhst. Useite bei den ♂♂ nicht so verschwommen rot, sondern kräftig gezeichnet und bei der Useite der ♀♀ ist ein helles Schwefelgelb der Grundfarbe ein sehr auffälliges Merkmal. Zwar ist auch bei *palina* das ♀ ziemlich kontrastreich gezeichnet, doch ist *palinoides*, wenn man die Tiere vergleicht, eine gut unterschiedene Form. Morphologisch ist ebenso wie bei allen geographischen Formen der *pales* kein Unterschied wesentlicher Art feststellbar."

This description was written by Reuss in part 3 of Draeseke's article on the collections made by the Stötzner expedition. The locality "Tat." was a contraction for Ta-tsien-lu.

Genitalia :—Pl. 24, fig. 111. There is nothing in the development of the genitalia in this race which calls for comment. Reuss's statement on morphology at the end of his description is quite mistaken, for he was including both *B. napaea* and *B. graeca* among the forms of *B. pales*. Even among the true races of *B. pales* a certain amount of subspecific specialisation exists, especially in the subsps. *aquilonaris* and *pyrenesmiscens*, and to a lesser degree in the more purely Himalayan group of subspecies.

Identification :—A glance at the figures on pl. 40 will show at once that subsp. *palinoides* is characterised by the shorter and broader form of its wings, and its smaller size and proportionately heavier black markings. It is further distinguished from subsp. *palina* by the great extent of the pale markings on the underside, especially on the hind-wings. The tendency for all the pale-yellow spots along the outer margin of the wing to run together, consequently obscuring the ground-colour to a great extent, gives the females a striking appearance; it is also a feature of the males, though less pronounced. Reuss in his description comments on the brilliant contrasts of the colouring on the underside of the hind-wings, but I do not find that this is actually any more pronounced than in subsp. *palina*. So far as I can ascertain, the female of subsp. *palinoides* does not produce a melanic form, as does subsp. *palina*. In spite of the proximity of these two races, there is no question but that they are quite distinct, and, as a comparison of the photographs on pls. 39 and 40 will show, there should not be any real difficulty in identifying them. Reuss's specimens were from the material obtained by Stötzner's expedition, and the two specimens I have figured are from that source also and probably topotypes. I have already noted that the two specimens of subsp. *palina* figured on pl. 39 also are topotypes. A comparison of these figures is therefore especially valuable, as they all come from the same district.

It is necessary to mention the name *tatsienlouna* Reuss (1925, *Int. ent. Z.* **19** : 280), which was described as "nov. sp. geogr."; but Reuss does not mention a female and, apparently, only had one male, the characteristics of which he notes as "mit ganz karminroter Unterseite der Hinterflügel und durchgehender, gezackter, silberglänzender Mittelbinde dieser Hinterflügel-Unterseite." The locality he gives is "Tatsienlou," which, taken with his remarks, makes it impossible to do other than place this specimen as an aberration of subsp. *palinoides*.

Distribution :—There is less information on the distribution of subsp. *palinoides* than of subsp. *palina*, but, like the latter, subsp. *palinoides* is not confined to Ta-tsien-lu. Some of the specimens lent me by Dr. L. G. Higgins were labelled Sung-pan-ting.

(9) *B. pales sifanica* (Gr.-Gr.).

Pl. 40, figs. 252–257.

Argynnis pales var. *sifanica* Groum-Grshimaïlo, 1891, *Hor. Soc. ent. ross.* **25** : 456.

Original description :—" Subtus alis pallidioribus, anticis maculis nigris distinctissimis, posticis magis versicoloribus.

" In montibus Sinin-Schan et Dshachar."

Genitalia :—Pl. 23, figs. 106, 107, 108. The form of the genitalia is as in the other races from Tibet and south-west China. In a single very large specimen in the British Museum, which superficially is only distinguished from normal subsp. *sifanica* by its much greater size, the genitalia were found to be decidedly larger also (fig. 108). Having only the one specimen, it is not possible to say if this increase in size is a racial characteristic, or only individual, but the probability is that it is racial. The head of the harpe in this specimen also assumes a very unusual form; but in this respect the chances are in favour of its being an individual variation.

Identification :—Subsp. *sifanica,* although unquestionably connected with the group of brightly-coloured races of Tibet and south-west China, is much less conspicuously coloured itself. On the upperside it is pale, and the black markings fine, while on the underside the same loss of vivid colour prevails, the ground-colour of the hind-wings being a dull cinnamon, the central band yellow with a slight suffusion of dark scales, and the marginal lunules yellow; the latter colour is the predominant tone. The female is similar but still paler. The actual pattern of the underside is most like that in subsp. *palina*, but the difference in size and brightness of colouring makes any confusion between the two impossible. From the subsp. *eupales*, which is about the same size, subsp. *sifanica* should be distinguished by its thin black markings, and much paler and less variegated underside coloration.

The figs. 256 and 257 (pl. 40) show the large specimen I have already mentioned in connection with the genitalia. As I have seen only the one example, and it is in every respect except size and the extent of the black spotting identical with subsp. *sifanica*, I include it here. But if a series were available, it is very probable that it would prove to be a distinct race. It will be noted that in size and the extent of the black spotting, this male is equal to the females of subsp. *palina*; the unknown female would probably be proportionately larger. The male came from the Leech collection, and is labelled " Hou-Kow, Thibet (Native coll.) 10,000 ft. VII–VIII, 1890." The dissection I made of the genitalia is in the British Museum (Slide No. 1531, B. C. S. Warren).

Distribution :—Subsp. *sifanica* is so far known only from the Amdo District in central Tibet. The flight period probably starts in late May; several specimens were labelled " June 1 " and " 2."

(10) *B. pales lucida* (B.-Haas).

Argynnis pales lucida Bang-Haas, 1927, *Horae Macrolep.* **1** : 52; pl. 5, fig. 18 (♂).

Original description :—" Habitat : China sept. occ. Kansu, Richthofen mont. westl. Liang-tschou, Juli 2500 m.

" Verglichen mit *sifanica* Grum. Gr. von Amdo : grösser, sowie ober- und unterseits heller gelbbraun gefärbt, bei einigen ♂♂ war das Vfl. Mittelfeld gelbweiss aufgehellt, bei einigen ♀♀ die Grundfarbe weisslich gelb."

I place this race here on the strength of Bang-Haas' description and figure. I have not seen a specimen, so cannot even say for certain if subsp. *lucida* really is a race of *B. pales*, or whether it may not belong to *B. napaea.* The description and the figure of the male suggest the former; the reference to the whitish-yellow ground-colour of some females suggests a race of the latter. This extraordinary pale ground-colour otherwise appears only in *B. napaea* subsp. *nearctica.*

(11) *B. pales korla* (Frhst.).

Pl. 41, figs. 258–263.

Argynnis pales korla Fruhstorfer, 1903, *Deuts. ent. Z.* "*Iris*" **16** : 306.

Original description :—" Differiert von allen bekannten *pales*-Rassen durch die ausserordentlich breiten Flügel, welche mit einem intensiven, violetten Schiller übergossen erscheinen.

" Alle schwarzen Zeichnungen sind stark reduziert, wodurch *korla* ein noch helleres Aussehen als selbst *sipora* Moore bekommt. Die schwarze Basalregion der Hinterflügel ist gleichfalls sehr beschränkt im Gegensatz zu *palina* und *eupales*.

" Durch die sehr helle Unterseite erinnert *korla* wiederum an *sipora*, hat jedoch weniger Schwarzfleckung als *sipora*.

" Die subdiscale Silberfleckung ist obsoleter, der braune Basalfleck jedoch viel dunkler.

" Die Basis der Hinterflügel ist reich hell graugrün beschuppt und differiert dadurch von den hellsten ♀♀ aus dem Engadin, von denen ich etwa 100 zum Vergleich benutzte.

" Die weisse Zeichnung der Hinterflügel, namentlich der subanale Fleck sind viel heller und breiter als bei *pales pales*.

" *Korla* bildet auf diese Weise ein Mittelglied zwischen *pales* und *sipora* und ist wegen der verbreiterten Flügel wohl die grösste, bisher bekannte *pales*-Form.

" Korla; ♂♀ Coll. Fruhstorfer."

Genitalia :—Pl. 18, fig. 78; pl. 24, figs. 112, 113. The genitalia in this subspecies and the next are a remarkable example of how little connection there is between the actual size of the insect and the size of the genitalia; for subsp. *korla* is the largest known race of *B. pales*, and subsp. *generator* is only a little smaller, and yet the genitalia are no larger than in subsp. *sipora* (compare figs. 78 and 80), which is the smallest, and do not equal in size those of many other western races. In addition to the remarkable size, the ventral curvature of the claspers is another character in subsp. *korla* which points to its affinity with the Himalayan races. Variability in the shape and size of the head of the harpe is great and frequent; the photographs show three very different types.

Identification :—There can never be any difficulty in identifying subsp. *korla*; its great size and very red tone of orange ground-colour of the upperside, and the strong purple gloss on the upperside of the females (very slightly in some males also), render it quite unmistakable. The only race that makes any approach to it is the subsp. *generator*, some males of which assume a deeper tone of ground-colour upper and underside and can be practically as large; such examples are, however, abnormal, and even they can be identified without much difficulty.

Verity and others have taken for granted that ab. *darjana* Seitz ([1908] *Macrolep.* **1** : 230, pl. 68a) represents a race equal to any of the subspecies. That it is only a colour aberration of the male *korla* was pointed out by Wagner when he described his f. *juldussica*; but as this seems to have been overlooked, I may repeat, that in his description Seitz makes no mention of a female of *darjana*, and the only character he gives that would distinguish the male from subsp. *korla* is that it is a more " fiery red " than *generator*.

Distribution :—Fruhstorfer's specimens came from Korla, which is situated just a little to the south-east of the Yuldus Valley, in the extreme eastern Tian Shan. There is a long series in the British Museum that came from the Oberthür collection, all labelled " Fort Narine, Prov. Semirechgensee ", and some specimens taken by W. H. Evans from the " Koksu River, Tian Shan." The race therefore occurs in both the extreme western and eastern ends of the Tian

Shan : it seems probable that it exists in other parts of that great range also. I have no exact data as to the flight period ; it is probably in July and August.

(12) *B. pales generator* (Stg.).

Pl. 42, figs. 268–271.

Argynnis pales Schiff. var. *generator* Staudinger, 1886, *Ent. Ztg. Stettin* **47** : 235.

Original description :—" Die centralasiatischen *Pales*, die ich in Menge vom Alai (Margelan), Osch, Usgent, Namangan, Tianschan (Alphéraki) und vom dsungarischen Ala Tau erhielt, sind doch von den europäischen und denen vom Altai wie Tarbagatai so verschieden, dass sie besser einen eigenen Namen führen. Da ich vermuthe, dass sie die Stammform aller anderen *Pales*-Varietäten sind, nenne ich sie *Generator*. Sie sind durchschnittlich etwas grösser und breitflügeliger als *Pales*. Besonders aber sind die *Generator* ♂ weit greller braunroth und weniger schwarz gezeichnet. Auch die ♀ sind blasser, mit weniger Schwarz, und zeigen nur selten die grüngraue Färbung der aberr. *Napaea* Hb., und dann nur auf den Vdfln. Sie zeichnen sich noch durch weissliche Randflecke der Htfl., die meist nur am Innenwinkel stehen aus. Die Unterseite ist bei den ♂ braunroth und gelb gemischt wie meist bei *Pales*; bei den ♀ ist sie grünlicher gelb, mit weniger Rothbraun als bei *Pales*. Ich versandte diese Stücke bisher als var. *Isis*, doch können sie dazu nicht gezogen werden."

Genitalia :—Pl. 18, fig. 79 ; pl. 24, figs. 114, 115, 116. The few remarks made on the genitalia in subsp. *korla* apply equally to subsp. *generator* ; nothing further need be added.

Identification :—Subsp. *generator* is best distinguished by its large size, relatively pale coloration (especially in the females), and very reduced black spotting on the upperside. The ground-colour of the underside is most often a dull orange-yellow, not inclining to the redder tone of subsp. *korla*. The whole underside of the hind-wings is broadly washed with pale yellow, the areas of dark ground-colour being reduced, especially on the outer half of the wing ; the silver lunules are wanting, or almost so. There is very great variability in the markings of the underside, without, however, making any material difference in the general appearance. On the upperside the females also vary greatly, many specimens taking a pale green gloss of very varying intensity, which in certain localities becomes the predominant form ; in others it may be wanting, or very rare.

Distribution :—Subsp. *generator* has a very extensive geographical range. Staudinger recorded it from the Alai Mountains in the south, through the Tian Shan to the Dzungarian Ala-tau in the north (see original description) ; Verity (1932) from the Pamirs ; and there are many specimens in the British Museum from as far south as the Hindu-Kush and the Trans Alai Mountains. From what might be called the central area of its distribution, the Tian Shan, there are specimens taken by Haberhauer at Margilan in the west (Elwes coll.) ; and Wagner (1913) gives the following localities in the Ili district in the east : the valleys of the Taldi, Burchan and Usek (or Yssek), where it is said to fly from the middle of June to the beginning of August. It seems, like many Asiatic races, to inhabit great altitudes ; specimens in the British Museum are labelled 14,000 to 15,000 feet.

Subsp. *generator* f. *juldussica* (Wagner), pl. 41, figs. 264–267.

Synonymy :—*Argynnis pales* var. *juldussica* Wagner, 1913, *Ent. Mitt.* **2** : 115 ; *Argynnis pales* var. *graeca* Alphéraky 1881 (*nec* Staudinger), *Hor. Soc. ent. ross.* **16** : 409.

Original description :—" Während nun die ♀♀ dieser von mir als typische *Generator* aufgefassten Form einen durchaus einheitlichen Charakter bewahren (dunkelrotbraun mit deutlich ausgeprägter schwarzer Zeichnung) variieren dieselben bei einer aus dem Juldus-Gebiete erhaltenen grösseren Serie so ungemein, dass aus diesem Grunde allein schon eine Abtrennung der letzteren geradezu ein Gebot der Notwendigkeit ist. Da indes auch weitere nicht unerhebliche Unterschiede vorliegen, möchte ich sie als var. *Juldussica* von *Generator* trennen. Als Eigentümlichkeiten dieser könnten gelten : Das im allgemeinen geringere Ausmass, die beim ♂ öfters, beim ♀ immer bedeutend bleichere Unterseite aller Flügel, die oberseits stumpfer braune Färbung im ♂ Geschlechte und endlich das Aussehen der ♀♀. Die meisten weiblichen Individuen weisen ein *schwärzliches* Grün auf, das dem der var. *Napaeae* ungefähr entspricht, jedoch bis zu einem beinahe weisslich isabellfarbenen Ton abändern kann; dunkelrotbraune ♀♀ dagegen, wie ich sie aus den eingangs erwähnten Lokalitäten besitze, scheinen hier gänzlich zu fehlen, wenigstens lag mir kein derartig gefärbtes Exemplar vor."

(The localities referred to by Wagner in the last sentence are those already mentioned, on his authority, among the localities for subsp. *generator*; see above.)

I have already pointed out that females developing a remarkable pale green gloss seem to occur in many localities together with others without this gloss, and as this is the chief characteristic of f. *juldussica* it can scarcely be maintained as a race distinct from subsp. *generator*. In his description, Wagner states that a " blackish-green " suffusion suggesting " var. *napaea* " is usual in the females, but he qualifies this immediately afterwards by saying it varies to an almost white " isabel " (*i.e.* yellowish-grey) colour. From this I take it that the specimens I have already mentioned as having a pale, yellowish-green gloss, are one stage in the chain of colour variations which Wagner's series showed, terminating in his " isabel "-coloured examples. Judging from the colour range in the British Museum series, there can be no real doubt that when such a wealth of variability is present, females without any suffusion, that is in colour similar to the males, will also occur; this assumption is further supported by the fact that Staudinger in his description of subsp. *generator* refers to the occasional occurrence of females with a " grey-green " colouring like " *napaea* Hb.," which shows that the female of the race is dimorphic. On this character alone, then, it is impossible to uphold f. *juldussica* as a race; and the only other characters of importance, small size, and paler coloration of the underside, are present in subsp. *generator* in other localities, in small numbers of individuals. The specimens figured on pl. 41 agree closely with the description, though perhaps the ground-colour of the underside in these specimens is a little darker. Their small size is also obvious, if compared with figs. 268 and 270 on pl. 42; but the size is not constant in the series from either of the localities from which these specimens came. I have not seen specimens from the Yuldus Valley, and as it is always difficult to make certain of the appearance of a race from a description alone, there remains some slight doubt as to whether these specimens would agree exactly with Wagner's; but even if they did not do so, I doubt if the difference would be sufficiently marked to be of any consequence; small differences are quite a normal feature in a variable form if it occurs in a number of widely separated localities. The females from the Hindu-Kush are not as variable as those from the Juldus Valley evidently were; but, as in the parallel case of the dimorphic females of *B. napaea* subsp. *napaea*, we know that the frequency and degree of variability present changes in every locality, and it is certain that this will also be the case in f. *juldussica*. The name, therefore, must apply to any colony of subsp. *generator*, of which a proportion of individuals of both sexes are below the normal size, and the females exhibit a fluctuating degree of dimorphism: typical examples of subsp. *generator* will of course always occur in inverse proportion to the numerical abundance of the individuals of the form.

Distribution :—The form, as far as can be ascertained at present, occurs in the extreme east and the extreme west of the zone of the parent subspecies, *i.e.* in the Juldus Valley in the eastern Tian Shan mountains, and the Hindu-Kush in the west. There can be scarcely any doubt that between these extremes it exists in many other localities, very probably everywhere that subsp. *generator* occurs, though of course only as an aberration in many districts.

(13) *B. pales aquilonaris* (Stichel).

Pl. 42, figs. 272–277; pl. 43, figs. 278–281.

Synonymy :—Argynnis pales aquilonaris Stichel, 1908, *Berlin ent. Z.* **53**: 81, pl. 3, fig. 5; *Argynnis pales* var. *lapponica* Staudinger, 1871, *Cat. Lep. eur. Faungeb.* : 20 (in part); *Boloria pales hypoarsilache* Verity, 1932, *Deuts. ent. Z. " Iris "* **46** : 106; *Argynnis pales parvula* Collier, 1933, *Ent. Rundsch.* **50** : 55.

In the many cases of misapplication of names in entomology, none, perhaps, is stranger than that of the mythical race " *lapponica* Stg.", for the name seems to have been more or less forced on Staudinger by the entomologists of that time, after he had proved that no such race could be distinguished, and recorded that he had *not* taken it in Scandinavia. Ever since the publication of Staudinger's article (1861) almost every collector, of every nationality, who had visited Scandinavia, used the name, and most have triumphantly recorded the capture of " var. *lapponica* Stg.," yet, incredible as it may seem, no such race exists; the specimens reported as such invariably consist of an amalgamation of aberrant specimens of *B. napaea* and *B. pales* subsp. *aquilonaris*. Because of all this confusion, it is necessary to give a brief account of how and why the name originated.

In an article on a trip to Norway Staudinger (1861) dealt with the northern forms of *B. pales* among other species. He headed the paragraph on the former as :—

" Argynnis Pales S.V. et var. Arsilache Esp.
Lapponica."

By this, Staudinger was merely implying the Laplandian *B. pales* and its " var. *arsilache*." In the whole article he never mentions the word " Lapponica " again. He deals with the habitats and variation of what he calls " typical *arsilache* " and " *pales*," in Lapland, recording how both vary so much that every transition exists between the two, and that the differences between them are only those of colour, and the presence or absence of certain spots, and not of pattern. He ends by stating that he cannot accept them as distinct species, as it is impossible to distinguish them. In the entire account he never mentions the name " *lapponica*," and never refers to the existence of any other race than " *pales* " and " *arsilache*." Yet this article has been cited by every writer in the past eighty years, as including the original description of " var. *lapponica* " Stg.; some have even gone so far as to cite the characters alleged to have been given by Staudinger. It is not necessary for me to quote Staudinger's words here; anyone interested can easily look them up; but it is quite clear that Staudinger had no intention of naming any variety of *B. pales* in his article, and, in fact, he did not do so. But there is still a further point to note. He gave an index at the end of the paper (1861 : 403, 404) with a note at the head which runs: "Die von uns aus Norwegen mitgebrachten Arten sind gesperrt gedruckt." (*i.e.* the names of the species he and Dr. Wocke brought back from Norway were printed with the letters widely separated). Looking down the list, one finds the following:—

"Arsilache Esp.
Lapponica B.
Pales SV."

From this two facts are clear: (1) Staudinger was, at that time, under the impression that Boisduval had named a race "*lapponica*," and (2) he had *not* captured specimens in Norway that he considered could be referred to it. It must also be noted that in his 1861 Catalogue (published in September of that year) and therefore prior to his article on Finmark, which was published during October, November and December the same year, Staudinger gives on p. 9 a list of forms of *B. pales*, which includes "e.v. *lapponica*." (The "e" indicates the 5th var. of the species.) He gave no reference with this, so it may have been accepted as the publication of the name, though of course it would only be a nomen nudum. He may equally have intended to add the "B." as he did in his paper, but failed to do so. In spite of these facts, from that time on "v. *lapponica* Stg." came into general, if always completely vague, use. The result of this was that ten years later, Staudinger, in his second Catalogue (1871 : 20) included "v. *lapponica* Stg.," with the following definition: "transitus ad seq." The next var. was "*arsilache*." Since then the name has more or less existed; but to what did it refer? In his article (1861) Staudinger had taken the Scandinavian race of *B. pales* as "typical *arsilache*"; and his "*pales*" must have been *B. napaea*; so much is certain, for no other *Boloria* races exist in Scandinavia; and these two fly together as Staudinger described. The name, then, could only apply to aberrations of these species; and as "transitional" would mean opposite types of variation in the two cases, it is doubtful to which it should apply. This uncertainty is reflected in the series of insects collectors have assumed to be "v. *lapponica*"; aberrant specimens of one or both species, usually a mixture of the two. The correct solution of this jumble is, probably, that Staudinger's definition must be held as insufficient, and the first real definition accepted. This was that given by Lang (1884, **1**: 199; **2**: pl. 47, fig. 3). Lang makes it clear that he was applying "*lapponica* Stg." to some "var." that was *not* either of the two Scandinavian races of *Boloria* known to him; for he *designates these by other names*. He states that *lapponica* was "smaller than the type" (i.e. *pales* Lang *nec* Schiff. = *B. napaea*) and "close" to "*arsilache*"; thus implying a transitional form between these races, as Staudinger had done. Further, the localities he gives prove that he applied these names exactly as the latter did, also. He states that "*pales*" occurs "on moors and plains in North Russia and Scandinavia, also in Altai and N.E. Siberia," proving that *pales* Lang was *B. napaea*, for *B. pales pales* does not exist in any of these districts. Of "*arsilache*" he states that it occurs in "Germany, vallies in Switzerland, Scandinavia, N. and C. Russia and Siberia"; showing he employed "*arsilache* Esp." not only for the large German subsp. *alethea*, but also for the smaller subspecies from Switzerland, Scandinavia, Russia and Siberia, districts where subsp. *alethea* does not exist; a conclusive proof that Lang dissociated subsp. *aquilonaris* from his *lapponica*. The only locality he gave for the latter was "Lapland"; it is therefore incontestable that he believed a third race existed in the extreme north, and intentionally restricted the name to it. As such a race, however, never existed, *lapponica* Lang, as a racial name, is not valid. When dealing with such cases, the International Commission pointed out that names must be given to objects themselves, and not to our conception of the said objects, adding: "Names based upon hypothetical forms have, therefore, no status in nomenclature." These facts rule out all possibility of using "*lapponica* Lang" for either of the existing races, but it can be held to be the valid name of the one specimen figured by Lang, if the figure be dissociated from Lang's data and description. As such it is restricted to an insignificant aberration, of unknown origin, for the figure is so poor that one cannot be certain whether it should be connected with subsp. *alethea* or subsp. *aquilonaris*. Personally, judging from the coloration, I would refer it to a small N. German specimen of the former, as I do not think any such specimen ever came from Lapland. This is immaterial, however, for, as I have shown, if *lapponica* were used for either of these races now, it would be creating a new racial name, for it could not be "*lapponica* Lang." The facts prove that the wide-ranging subspecies of *B. pales* was unrecognised until Stichel described his race *aquilonaris*, which of course had years of priority over *hypoarsilache* Vty.

Original description:—"Eine bisher unbeschriebene Unterart der, glaube ich, am weitesten variationsfähigen Argynnide. Der allgemeine Eindruck fast wie ein kleineres Exemplar von *A. p. arsilache* Esp. (typ.) aus Deutschland.

"Oberseite der Flügel satt rötlich-braun, die gewöhnlichen Zeichnungen der Art sämtlich verstärkt, im Mittelfelde mitunter derart, dass die Flecke in der Breite des Flügels zu unregelmässigen Binden vereinigt und in der Längsrichtung zu ebensolchen Figuren zusammengeflossen sind. Die schwarzen Randflecke beider Flügel verbreitert, manchmal zu einem geschlossenen Saumstreif verflossen, namentlich am Distalrande des Hinterflügels, wo die anschliessenden schwarzen dreieckigen Flecke diesem Saumbande aufsitzen und nur teilweise durch feine Striche oder schmale Mondfleckchen von ihm getrennt sind. Wurzelfeld des Hinterflügels breit geschwärzt.

"Unterseite: Vorderflügel mit deutlichen schwarzen aber isoliert stehenden Flecken. Hinterflügel auffällig bunt; Grundfarbe vorwiegend rostrot, im Distalfelde mit ockergelb gemischt. Die dem rotbraunen Wurzelfeld folgende, von schwarzen Winkel- und Wellen-Linien eingefasste ockergelbe Querbinde auffallend schmal. Im Discalfeld eine Reihe undeutlicher Fleckchen; derjenige im vorderen Medianzwischenraum ringartig, mit weissem oder weisslichem Kern. Dieses Zwischenaderfeld, welches bei *A. pales* typ. meist auffällig gelblich abgetönt ist, hier—ähnlich wie bei *A. p. arsilache*—nur wenig heller als der übrige distale Flügelteil. Am Distalsaume steht eine Reihe von Silberfleckchen, die übrige Flügelfläche ist ziemlich spärlich silberfleckig, mitunter ist nur ein runder Fleck an der Wurzel hinter der Mediana und ein länglicher Fleck am Zellschluss erhalten.—Nach 3 ♂♂ der Ausbeute, Gellivara, coll. Ragnow."

Stichel was uncertain when he wrote this description whether this insect was a purely local form, or the one usually identified as "*arsilache*" in the north. His figure is conclusive proof that his specimens were typical of the Scandinavian race.

Here one must point out that the subsp. *parvula* Collier, is unquestionably a synonym of Stichel's insect. The original description is as follows:—

"Eine *arsilache*-Form, die aber erheblich kleiner als *arsilache* Esp. ist und kaum die Grösse von *palina* Fruhst. erreicht. Da nach mündlicher Mitteilung des Herrn Ragnow diese kleine Form an ihrem Fundort allgemein vorkommt, dürfte es sich jedenfalls um eine konstante Form handeln. 2 ♂♂, 2 ♀♀. Ragnow leg. Fundort: Menz (Norddeutschland)."

It will be seen that small size is the only feature distinguishing Collier's *parvula* from subsp. *alethea* (i.e. *arsilache* Esp. as used by Collier), of which it is said to be a form. From this fact, and the locality, it is clear Collier was only redescribing subsp. *aquilonaris*, of which small size is also one of the principal characters; and though the latter varies a little in size in different localities, it is always one of the smallest races of *B. pales*.

Genitalia :—Pl. 25, figs. 118–123; pl. 26, figs. 124–128. The development of the genitalia in this race and the following is noteworthy for the ventral curvature of the head of the harpe. I have already shown that this feature is a characteristic of the subspp. *nearctica* and *nikolajewski* of *B. napaea*; but it is developed to a greater extreme in subsp. *aquilonaris* and subsp. *alethea*, and indeed is so pronounced, and of such frequency, that it might suggest a constitution specifically distinct from the other *B. pales* races. This, however, is certainly not the case. Although frequently present, it is not constantly so; in many examples the ventral line of the head is as flat as in the typical subsp. *pales*, also the degree of curvature, as can be seen by a glance at the figures on plates 25 and 26, is quite inconstant. Sometimes it is so extreme that the ventral line of the head rises above the dorsal ridge of the clasper, between the distal prong and the terminal apex of the clasper; but even this formation can occur at times in other races of the species (see pl. 21, figs. 95 and 96, subsp. *pales*; pl. 23, fig. 109, subsp. *palina*; pl. 24, fig. 114, subsp. *generator*). In other cases, as already noted, there is practically no curvature present.

A more important development is that the wings of the phallobase tend to be more widely separated at the proximal end, and somewhat more flattened distally. These two features, however, are again purely subspecific deviations of inconstant nature; they are not confined to these two races, though more frequently found in them.

Identification :—This little race is extremely close to the larger subsp. *alethea*. The type of pattern is the same in both; but in size, intensity of colour of the underside of the hind-wings, and extent of development of the black spots on the underside of the fore-wings, subsp. *aquilonaris* never equals subsp. *alethea*. It seems clear that subsp. *aquilonaris* is an alpine and arctic product; the subsp. *alethea* inhabits lower altitudes and latitudes. There are localities where a collector who is not familiar with the insects might find it difficult to say to which race the local one belonged; but on the whole the characters of size and coloration are sufficiently constant to make identification certain. In both races the colour of the underside of the hind-wings is a very dark red-brown, verging on orange-brown, and there usually are purple shades surrounding the dark submarginal spots, between the central band and the margin of the wing. The width of this premarginal area, from the external edge of the central band to the silver marginal lunules, is decidedly greater in these races than any others, and is a feature which distinguishes them very obviously. On the whole the ground-colour of the underside of the hind-wings is darker in subsp. *alethea*, and the black spots on the underside of the fore-wing heavier, than in subsp. *aquilonaris*. The difference in size between the largest individuals of the former and the smallest of the latter is great (compare pl. 43, figs. 279 and 280 with figs. 283 and 284); but subsp. *alethea* varies a good deal in size, and smaller forms like the Bavarian examples (pl. 44, figs. 290–293) are only slightly larger than the largest specimens of subsp. *aquilonaris*. But if the figures of the Bavarian specimens are compared with the Scandinavian specimens shown on pl. 42, in spite of the approximation in size, the heavier black spots on the upper and underside of the fore-wings of the Bavarian specimens (compare pl. 44, fig. 291 with pl. 42, fig. 277, both males; and pl. 44, fig. 293 with pl. 42, fig. 275, both females) are sufficient to distinguish them; and it must be stressed that these are the two extremes (the largest of subsp. *aquilonaris* and the smallest of subsp. *alethea*), yet they do not merge. The specimens from the Harz Mountains are more typical of subsp. *alethea* (pl. 43, figs. 286, 287 male; pl. 44, figs. 288, 289 female), and here the difference is unmistakable.

Subsp. *aquilonaris* varies a good deal in the extent to which the black spots on the underside of the fore-wings are developed. While never extremely heavy as in subsp. *alethea*, and normally more pronounced in the females than the males, they are sometimes considerably reduced, and even lost. It is such specimens that many writers have recorded as *B. pales*, and Staudinger (1861) affirmed to be indistinguishable from subsp. *pales* of the Swiss Alps; a totally mistaken idea, for in spite of the loss of these spots, the insect never assumes any really close resemblance to subsp. *pales*, on account of the characteristic markings of the underside of the hind-wings, where the broad, pre-marginal area, into which the marginal markings only extend to a very limited extent instead of more or less filling it, gives an especially distinctive appearance which can never be mistaken.

Habitat and Period of Flight:—The subsp. *aquilonaris* is essentially a marsh insect, and is never found at any great distance from swampy ground. In such localities, however, it is not confined to the most watery areas, but ranges into drier ground in the immediate neighbourhood. Here it often flies with *B. napaea* subsp. *napaea*, in central Europe, with the latter and its f. *frigida*, in Scandinavia and Lapland, and with the f. *frigidalis* in central Asia. In this region, Elwes (1899) writes that he found it at 6000 feet; and in the "Bashkaus country in flat, swampy forest at 4000 to 5000 feet." He adds that he found no real peat bogs in the Altai, but that "*arsilache*" appeared confined to swamps. The "*pales*" he mentions at the same locality were *B. napaea* subsp. *altaica*. It is remarkable that the maximum altitude at which Elwes found the subsp. *aquilonaris* in the Altai was 6000 feet, the same level as the highest point it attains in the Swiss Alps.

The flight period ranges from late June well into August, and varies considerably according to altitude. In a general sense it can be said that the drier the locality, the less intense the coloration, and the weaker the development of the black markings.

Distribution:—Subsp. *aquilonaris*, although not very generally distributed, has a greater geographical range than any other race of the species. It is most frequent in northern Europe, being distributed throughout Scandinavia, Finland and northern Russia; in this region it is the only race of *B. pales*. As one comes south, it becomes much less frequent and very local. It flies at Hinterzarten in the Black Forest, and probably in some districts in the Bavarian Highlands, though I have not seen specimens from the latter region. The form from the Schliersee recorded as intermediate between "*arsilache*" and *B. pales* by Osthelder (1925) is almost certainly referable to subsp. *aquilonaris*. In Switzerland it occurs in the Jura and in very restricted areas on the margins of small mountain lakes in the Cantons of Vaud, Bern and Grisons, also on the moors near Einsiedeln in Schwytz. Seitz (1909) records it (under the name of "*lapponica* Stg.") from Belgium, but all the specimens I have seen from that country are referable to the subsp. *alethea*. It is also probable that the record of the occurrence of "*arsilache*" at Larch in the Basses Alpes by Rowland-Brown (1914) is a mistake; the only French specimens I have seen were from the Limoges district in the west, and the Doubs in the east. To the east of Switzerland, while it is possible that subsp. *aquilonaris* may exist in certain restricted localities in the Austrian Alps, I know of none; but the description of specimens from Kainischmoor in Styria, given by Galvagni and quoted by Hoffmann and Klos (1914), strongly suggests subsp. *aquilonaris*.

In central Asia the race reappears again in the Altai Mountains, where it was taken by Elwes. These are the only Asiatic specimens I have seen. Verity stated (1932) that subsp. *aquilonaris* (= his *hypoarsilache*) extends its range to the Pacific. He gives no exact localities, nor any details to support this statement, which seems very questionable.

(14) *B. pales alethea* (Hemming).

Pl. 43, figs. 282–287; pl. 44, figs. 288–293.

Synonymy :—*Argynnis pales alethea* Hemming, 1934, *Stylops* **3** : 97; *Papilio arsilache* Esp. var. [1780] *Die Schmett.* **1** (Bd. 2) : Forts. 36; pl. 56, fig. 5 ♂ (the "*Argynnis pales arsilache* Esp." of many authors). *Papilio arsilache* Hübner, 1799, *Samml. eur. Schmett.* pl. 7, figs. 36, 37 (primary homonym of *Papilio arsilache* Esper (as above), and *op. cit.* Forts. 35; pl. 56, fig. 4 ♂.

Original description :—" This name is required for the insect described and figured by Esper, 1780, *Die Schmett.* **1** (Bd. 2) Forts. Tagschmett. : 36, pl. 56, fig. 5 ♂) as *Papilio arsilache* Esp. var. This insect has since become widely known as *arsilache* Esp., but this use of the name cannot possibly be justified, as *Papilio arsilache* Esp. (*ibid.* : 35, pl. 56, fig. 4 ♂) is an entirely different subspecies of *pales* Schiff. It was described from a specimen taken near Vienna, and is identical with nominotypical *pales* Schiff., to which, therefore, *arsilache* Esp. falls as a synonym. The specimen that Esper called '*P. arsilache* var.' came from Neustadt-an-der-Aisch in Lower Franconia, which is, therefore, the type locality of *alethea*, Hemming."

It is strange how many writers who have endeavoured to uphold the name "*arsilache* Esp." have completely ignored the salient fact that Esper gave the name to subsp. *pales*, and never gave any name to the race he figured as a variety.

Genitalia :—Pl. 24, fig. 117; pl. 26, fig 129; pl. 27, figs. 130–132. The characteristics of the curvature of the head of the harpe, and the tendency to distal flattening at the extremities of the wings of the phallobase in subsp. *alethea*, have already been described in connection with subsp. *aquilonaris*. There remains one other subspecific character to note, which also affects the free extremity of the harpe. In subsp. *alethea* the range of spine development on the head is, in a majority of cases, somewhat greater than in other *B. pales* races, though still falling short of that in *B. napaea*. This is, in a lesser degree, true also of subsp. *aquilonaris*. In this respect subsp. *alethea*, with subsp. *aquilonaris*, form a transition between the main group of *B. pales* races and *B. napaea* races; but although in a very few individuals the spinal range equals half the total length of the harpe, thus attaining the average range of *B. napaea*, the majority fall considerably short of this, and come well within the range normal to the *B. pales* races. The other characteristics of general development, size of saccus and wings of phallobase and aedeagus, are of course all typical of the *B. pales* specific group.

Identification :—The subsp. *alethea* is best differentiated from subsp. *pales* by the markings of the underside of the hind-wings, which have already been described as distinguishing subsp. *aquilonaris*, these markings being identical in the latter and subsp. *alethea*. The largest forms of subsp. *alethea* are also distinguished by their great size, and the heavy black spots of the underside of the fore-wings characterise all forms of the race. The differences which distinguish subsp. *alethea* and subsp. *aquilonaris* have already been noted (see above).

Habitat and Period of Flight :—Everything noted in respect of the habitats and habits of subsp. *aquilonaris* apply equally to subsp. *alethea*; there is nothing further to add. Subsp. *alethea*, however, inhabiting as it does lower levels and more southerly latitudes, appears on the wing slightly earlier in the season.

Distribution :—The geographical range of subsp. *alethea* is very restricted. Northern and central Germany comprise the area of its most frequent occurrence. Here it is widely distributed in suitable districts. It extends westward into Denmark and Belgium, and east to the Bavarian Highlands, and into Austria. Hoffmann and Klos (1914) mention a number of localities in Styria, which seem to be the most southerly and easterly habitats one can accept for certain. Heyne (1895) gives the Tatra, but this requires confirmation. Verity (1932) states it occurs " locally in Siberia," but gives no exact localities; it is probable this record is the result of confusion with subsp. *aquilonaris*.

(15) *B. pales banghaasi* (Seitz).

Pl. 44, figs. 294, 295.

Argynnis pales form *banghaasi* Seitz, 1909, *Macrolep.* **1** : 230, pl. 68, a.

Original description :—(From English edition). " Whereas the forms from Central Asia mentioned above belong to the *pales*-series, a form from Kentei which Herr Bang-Haas has kindly sent me is an *arsilache*; its upperside is very strongly spotted with black, the fore-wing beneath bearing weak spots and the hind-wing being very silvery. I name it *banghaasi* form nov. (68, a)."

Genitalia :—Pl. 27, fig. 133. While the structural development in subsp. *banghaasi* is typical of the *B. pales* races in general, it is suggestive in minor details, such as the formation of the proximal dorsal prong of the clasper of subsp. *pyrenesmiscens*. In the latter and subsp. *banghaasi* this prong tends to be heavier in build. In both these subspecies, also, the range of the spinal development on the head of the harpe can attain an extent equal to that in subsp. *alethea*; indeed subsp. *banghaasi* is to some extent transitional between subsp. *alethea* and subsp. *pyrenesmiscens*.

Identification :—I know this subspecies only from three specimens in the British Museum, two males and one female. Judging from these, the broad clear (*i.e.* unsuffused) yellow central band on the underside of the hind-wings is one of the most striking features of the race, and when taken in conjunction with the faint marking of the black spots on the underside of the fore-wings, as compared with the extensive development of these spots on the upperside, makes a combination of characters which gives the race a readily recognised appearance. In the male specimen figured the silver spots on the underside of the hind-wings are only weakly developed, and the ground-colour is a deep cinnamon; it is a somewhat paler shade in the female, and the silver spots are more pronounced.

Distribution :—So far known only from the Kentei mountains. The female in the British Museum is labelled " Odessa "; this, it seems certain, must be a mistake.

(16) **B. pales pyrenesmiscens** subsp. n.

Pl. 44, figs. 296, 297; pl. 45, figs. 298–301.

Synonymy :—*Boloria pales* race *pyrenesmiscens* Verity, 1932, *Deuts. ent. Z.* " *Iris* " **46** : 102, 109 (*nomen nudum*).

Note :—Verity (*loc. cit.*) quotes Higgins (1930, *Entomologist* **63** : 200) incompletely as follows: " . . . the *pales* from the Pyrenees is to some extent intermediate in the general facies of the butterfly and in the shape of the genitalia, but rather resembles *pales*." Verity then adds: 'it will, by the way, be well to have the name *pyrenesmiscens* to designate this interesting race (series of cotypes from Gèdre, Hautes Pyrénées, in my collection).'

As Verity's reference to this race (quoted above) does not constitute a valid description under Article 25 of the International Rules of Zoological Nomenclature, I am obliged to treat the race as undescribed, and adopt Verity's name for it.

Genitalia :—Pl. 27, figs. 134, 135; pl. 28, figs. 136–141. Perhaps the most striking development in this subspecies is the immense variety in the form of the head of the harpe; this variability is so prevalent that it can be said to surpass that known in any other race of the species, with the possible exception of subsp. *pales*. In some examples the formation resembles that in subsp. *aquilonaris* (like figs. 137, 139, 140); others are more like subsp. *pales*, and yet others suggestive of *B. graeca* (like figs. 134, 136, 141). It was doubtless specimens like the latter that led Higgins (1930) to suggest that subsp. *pyrenesmiscens* was in some degree transitional between *B. pales* and *B. graeca*. But, as I have shown in part IV, such examples are not in any real degree transitions towards *B. graeca*, but still absolutely within the range of variation appertaining to *B. pales*. The short head of the harpe is of course the only feature that suggests this idea; but if these specimens are examined the head will be found to represent a greater extent of the total harpe length than does the head in the average individual of *B. graeca*. The more reduced proportions in the latter are the normal ones, while in subsp. *pyrenesmiscens* the specimens with a short head are the extremes in that direction; the opposite extreme is shown in figs. 137 and 140, and intermediate forms represent the normal. Further, any idea of transition is at once disposed of by the full development of the wings of the phallobase, for these processes are of full dimensions and show no tendency to reduction towards the specialised form they assume in *B. graeca*. It may be noted that all types of harpal head form can occur in individuals from any one locality. Thus figs. 136–140 are all from specimens taken at Gavarnie; they can be matched by specimens from the eastern Pyrenees, or the Cantabrians.

Identification :—Subsp. *pyrenesmiscens* in pattern and colour seems to be an amalgamation of the features of subsp. *pales* and subsp. *alethea*. The colour of the upperside is very similar to that in subsp. *pales*, and the black spotting almost identical; on the underside the male is again very close to subsp. *pales*, though the ground-colour of the hind-wings is on the whole less brilliant, and more yellow in tone, while on the fore-wings the prominent black spots recall subsp. *alethea*. The same features characterise the female, but the whole underside is much paler, yellow or yellowish-green often obliterating the normally dark areas on the hind-wings. In some examples, however, the red-brown ground-colour is still well in evidence, but such specimens are the exception. The black spots on the underside of the fore-wings are heavier than in the male, and on the whole the markings of the underside are less sharply defined in both sexes than in subsp. *pales*. The pale coloration of the underside and the extent of the black spots on the underside of the fore-wings are the only points of resemblance to *B. graeca*, all other characters are those of *B. pales*.

Habitat and Period of Flight:—Subsp. *pyrenesmiscens* frequents localities of the same type as those in which one finds subsp. *pales*, at levels between 4000 and 7000 feet. Cooke (1925) records that he found subsp. *pyrenesmiscens* emerging at Gavarnie as early as 10 June; later, 16 July, he found it in great numbers near the Col du Tourmalet, up to 6500 feet, in perfect condition. The date of emergence, therefore, is evidently very dependent on the altitude. Most often the insect is recorded in July, and I have myself found the male just emerging at about 5500 feet in the mountains above Eaux Bonnes, below the Col de Lurdé, on 10 July. As a month seems an exceptionally long time for emergence to be retarded by about 1000 feet difference in altitude, and considering the fact that subsp. *pyrenesmiscens* is abundant at Gavarnie at the very end of July and must often be on the wing there in early August, I think that 10 June must be a somewhat exceptional date. The specimen from the Picos de Europa (pl. 44, fig. 296) was taken by Higgins at 6000 feet on 5 July, and he found the race in numbers at Pajares a few days later, so that from east to west there does not appear to be any change in habits or habitats.

Distribution:—Subsp. *pyrenesmiscens* is confined to the Pyrenees and the Cantabrian Mountains; it seems to be well distributed through those ranges. The holotype (male) in the Warren collection, came from Gavarnie; a number of paratypes are also from that locality and Eaux Bonnes.

3. *Boloria graeca* (Stg.).

Argynnis pales var. *graeca* Staudinger, 1870, *Hor. Soc. ent. ross.* **7**: 61; pl. 1, fig. 4 ♀.

Composition of species:—The species, which is purely a western one, includes three (possibly four) subspecies; two confined to the Balkans, and one (or two) to Italy.

(1) *B. graeca graeca* (Stg.).

Pl. 45, figs. 302–305.

Original description:—" . . . Uebrigens sind die griechischen Stücke hier noch bedeutend grünlicher als die caucasischen. Die Oberseite der ♂♂ ist gelbroth, etwa wie bei *Arsilache*, die der ♀♀ mit einem starken Anflug von grüngelb, wie bei hellen *Pales* ♀♀; die Franzen der griechischen Stücke sind fast weiss und schwarz gefleckt, während sie bei den Caucasieren wie bei *Pales* und *Arsilache* röthlich bleiben. Man könnte schon deshalb die griechische Form für sich als var. *Graeca* aufführen."

The " hier " in the first sentence of this description refers to the underside of the hind-wings.

Genitalia:—Pl. 29, figs. 142, 143. From the point of view of structural development, there can be little doubt but that *B. graeca* is the most specialised species of the genus. The outstanding feature is the change in proportional development of the phallic organs relative to the other parts; and though the reduced size of the aedeagus is itself quite remarkable, the important point is that this reduction is not proportional to the still greater reduction in the size of the wings of the phallobase. We have, therefore, clear evidence of two distinct evolutionary changes, both operating independently, on different though associated organs, to bring about a change in relative proportions in a manner that has no counterpart in the organic development of the other *Boloria* species. Indeed, in all the Argynnid genera I have so far examined, the only other case of marked alteration in the relative proportions of associated parts of the genitalia that I have found is in *Argyronome laodice*, where, however, the alteration has been in the reverse direction, the phallic organs having increased in size to an extent that is scarcely credible (see p. 9). But even in this case the relative proportions of the aedeagus and phallobasic wings have been maintained.

These facts emphatically override any possible arguments that can be brought in support of the contention that *B. graeca* and *B. pales* are conspecific. The result of the change in proportional size is very obvious in the frail and narrow wings of the phallobase; a less obvious change is that these wings do not originate from the basic plate in the same manner as in the other species, but are connected with it by a short stem. This feature is easily defaced by pressure in mounting the specimen, so that it is not apparent in some of the photographs. Pl. 29, fig. 145 gives a good idea of the actual form. In addition to these characters, the spinal range on the head of the harpe averages three-tenths of the total length of that process, the lowest average in the genus. Though quite obvious, owing to the corresponding reduction in the length of the head, this character is insignificant in comparison with the others. There is less variability in the form of the head of the harpe than in the other species.

Identification :—Like all the races of *B. graeca*, the typical subspecies is easily distinguished from *B. pales* races by the distinctly ocellated spots on the underside of the hind-wings, and the almost straight costa and outer margin of these wings. Subsp. *graeca* is further distinguished by the extremely pale, often greenish tone of the underside, and the heavy black spots on the underside of the fore-wings. On pl. 45, figs. 306 and 307 show a Balkan male of *B. pales* subsp. *pales*; this will enable the difference of the curvature of the costa and outer margin of the hind-wings to be contrasted with the straight lines in *B. graeca*, figured just above them. The general difference in colouring and the black spots on the fore-wings are also obvious. On the upperside, the female is often much paler than the male; the difference in shade can even be noticed in the photograph (pl. 45, fig. 304).

Distribution :—Subsp. *graeca* is apparently confined to the mountains of Greece.

(2) *B. graeca balcanica* (Rbl.).

Pl. 46, figs. 308–313.

Argynnis pales Schiff. var. *balcanica* Rebel, 1903, *Ann. nathist. Hofmus. Wien* **18** : 169.

Original description :—" Im Rilogebiete häufig in der alpinen Zone (bei ca. 2000 m.), auch auf dem Gipfel des Vitos (Buresch-Drenowski, Juli 1902). Die Stücke stimmen nach Elwes mit solchen aus den Hochgebirgen Bosniens überein und unterscheiden sich auf der Unterseite von typischen alpinen Stücken durch die deutliche schwarze Zeichnung der Vorderflügel und die deutliche Ocellenbildung der Hinterflügel. Die Form nähert sich darin der grösseren und bleicheren Form *Graeca* Stgr. und kann am besten als var. *Balcanica* bezeichnet werden.

" Dieselbe Form wurde kürzlich auch in Rumanien bei Sinaia gefunden (det. Rbl.)."

Genitalia :—Pl. 29, figs. 144, 145. The structure of the genitalia is so uniform in the various races of *B. graeca* that the description given for subsp. *graeca* covers all that need be said.

Identification :—Contrary to what has been suggested by several writers, I cannot say that I find it difficult to distinguish subsp. *balcanica* from *B. pales* subsp. *pales*. Drenowski (1925) states that some subsp. *balcanica*, especially from the Rilo Mountains, are very similar to *B. pales*, and others have made similar comments. Elwes (1900) describes subsp. *balcanica* as transitional between the subspp. *pales* and *caucasica* of *B. pales*, but he evidently had not realised that his series of specimens included subsp. *pales*. The specimens shown in pl. 45, figs. 306 and 307 were taken by him in the Rilo Mountains, as were the specimens of subsp. *balcanica* shown in pl. 46, figs. 308–311, at the same altitude and within a day or so of each other. Thus the two species may have been flying on the same ground. On comparing these specimens the differences between them will be easily noted; the costa and outer margin of the hind-wing curved in subsp. *pales*, flattened in *B. graeca* subsp. *balcanica* to the extent of the outer margin becoming almost concave near the apex in the male, etc. Others have probably made the same mistake Elwes did, and overlooked the fact that *B. pales* was present among their supposed subsp. *balcanica*, which would account for many of the confused statements regarding the latter.

Subsp. *balcanica* differs from subsp. *graeca* in being slightly smaller, the black spots on the upper and underside of the fore-wings not quite so strongly marked, the ground-colour underside hind-wings darker in both sexes, the central band a brighter yellow, the whole appearance much more variegated. There is a considerable amount of variation in the coloration of the underside, especially in the females, but even in large and pale examples, like pl. 46, figs. 310, 311, the variegated appearance of the underside is still distinctive. In size, too, there seems to be a greater range of variation than in the other races, but it will be noted that the very small female (pl. 46, figs. 312, 313), though smaller than the male *B. pales* from the Rilo, retains the characteristics of subsp. *balcanica* most unmistakably.

Distribution :—Subsp. *balcanica* is widely distributed in the Balkans; Rebel (1903, 1904, and 1913) recorded it from Bulgaria, Roumania, Bosnia, Hercegovina, Montenegro, Albania and Macedonia. Drenowski (1925) states that subsp. *balcanica* is most abundant in sub-alpine zones, occurring between 1800 and 2000 m. on Mt. Witoscha, at 1400–2400 m. in the Rilo, and 1000–2400 m. in the Perim Mountains. At that time he had no records of its occurrence in the Stara Planina or Rhodope ranges (in the former he included the Balkan Mountains, and by the latter implied the south-eastern chain, as distinct from the Rhodope Planina and Perim Dagh). He thought it likely that the race would be found in these ranges in the future. Haig-Thomas (1936) recorded " *A. graeca* " (*i.e.* subsp. *balcanica*) on the Belmeken in the Rhodope Mountains, which, of course, is not the region referred to by Drenowski, who would have included it in the Rilo range.

(3) *B. graeca brogotarus* (Frhst.).

Pl. 46, figs. 314–317.

Synonymy :—*Argynnis pales brogotarus* Fruhstorfer, 1909, *Int. ent. Z.* **3** : 112; *Argynnis graeca tendensis* Higgins, 1930, *Entomologist* **63** : 199; pl. 2, figs. 3, 4, 7.

Original description :—" ♂ grösser als 150 Exemplare aus anderen alpinen Fundorten meiner Sammlung; die Apikalpartie der Vorderflügel und die Submarginalpunkte der Hinterflügel wesentlich markanter. Die weisslichen Distalflecke der Hinterflügel-Unterseite auffallend vergrössert.

" Alpes maritimes, Col di Tenda, Juli 1908, 3 ♂♂."

Although not very detailed, this description cites the chief characters of this race of *B. graeca*; the feature of the extended white apical spot on the underside of the hind-wings is especially characteristic of all races of the species. In *B. pales* this spot is set about its own width from the costal spot of the central band, and separated from the outer margin by a broad space of the dark ground-colour. In *B. graeca* it almost unites with the silvery marginal spot at the apex. This is very obvious in figs. 315 and 317 (paratypes of *tendensis* Higgins), and makes a striking contrast with the male *B. pales* subsp. *pales*, pl. 45, fig. 307; the marking of this area of the wing is very constant in the latter.

Genitalia:—Pl. 29, figs. 146, 147. As in the case of the subsp. *balcanica*, the description of the genitalia given with the typical race applies equally to subsp. *brogotarus*.

Identification:—Subsp. *brogotarus* is closest to subsp. *balcanica*. The underside of the hind-wings tends to become suffused with greenish in a more pronounced manner than in subsp. *balcanica*; the black spots on the upperside, especially the submarginal row in the male (and in some females), are larger; the fore-wings tend to be shorter, and do not extend far beyond the hind-wings, giving the insect a squarer appearance.

Subsp. *brogotarus* differs from *B. pales* subsp. *pales* as do the other races (see notes above, on the apical spot of the hind-wings), and even if the two were taken on the same ground, identification should be simple.

Distribution:—Subsp. *brogotarus* appears to be confined to the south-eastern areas of the Maritime Alps. It was taken on the Col di Tenda by Fruhstorfer and Higgins, and recorded by the latter from St. Martin Vesubie. The specimens Verity described from Mt. Lega, and those taken by him above Valdieri (1932), prove that subsp. *brogotarus* occurs in those localities, and very possibly flies there with *B. pales* f. *mixta*.

Subsp. *brogotarus* f. *medioitalica* (Trti.).

Synonymy:—*Argynnis pales medioitalica* Turati, 1911, *Ann. Mus. zool. Napoli* (n.s.) **3** : 21; *Argynnis pales* Schiff. Rasse *majellensis* Dannehl, 1933, *Ent. Z.* **46** : 244.

Original description:—" Il ♂ non più grande della forma *palustris* Frhst. dell' alta Engadina e del Sempione, ne ha medesima disposizione e grandezza di punteggiatura, ma un colore più dilavato, giallognolo anche.

" La ♀ appena leggermente velata di atomi oscuri molto meno della *isis* Hb. e della *palustris* Frhst. reca i margini distali formati da una linea di punti, come nel ♂, al termine di ogni costa, e fra essi un interstizio giallognolo chiarissimo.

" Disotto traspajono leggermente tre punti della linea antemarginale: gli apici sono di un giallo di zolfo chiaro pochissimo frammisto di rosso, cosi pure i disegni delle ali posteriori, con tuttavia i contorni più segnati che nella *isis* Hb., e le macchie perlacee meno brillanti, quasi opache, più piccole.

" Due esemplari del Gran Sasso d'Italia: . . ."

" . . . Nella mia collezione ho una ♀ identica a quella del Museo di Napoli raccolta alla Majella il 6 agosto 1907: . . ."

Genitalia:—Unknown.

I have never seen specimens of this insect, but from the description and locality it seems probable that it is a dwarf race of *B. graeca* and not of *B. pales*. As it was described from only three specimens, it remains uncertain if it can claim to be a genuine subspecies, or is only a form of the subsp. *brogotarus*. The latter seems the most probable, for there is little in the description to suggest that it differs in any marked degree from subsp. *brogotarus*, with which Turati neglects to draw any comparison. There are also instances in other species of races of the Maritime Alps appearing in dwarf form in the Abruzzi. The f. *belzebub* of *Erebia pluto* is a well-known example.

The only localities, other than those given by Turati, from which this form has been recorded, are the Montagna Grande, Mt. Amara at 2300 m., and Mt. Genzana given by Dannehl for his race *majellensis*.

Note :—There remain two *Boloria* races that have not been mentioned in this revision. Up to the summer of 1939 I had not been able to get material of either, without which it was impossible to determine their true affinities. The war then put an end to any possibility of doing so. The races are :—

(1) *Argynnis pales neopales* Nakahara, 1926, *Insect. menst.* **14** : 48, which was introduced in place of *Argynnis pales sachalinensis* Matsumura, 1925, *J. Coll. Agric. Hokkaido Imp. Univ.* **15** : 100, pl. 8, fig. 14 (male) ; the latter being a homonym. The locality of the type was given by Matsumura as " North Saghalien, Rikovskoie."

(2) *Argynnis pales contempta* Zerny, [1932], *in* Rebel and Zerny, in 1931, *Denkschr. Akad. Wiss. Wien* **103** (2) : 70 ; from Montenegro and Albania.

Probably *neopales* will prove to be a race of *B. napaea*, but one cannot be certain, and it might only be a form of some other subspecies. The position of *contempta* is far more uncertain, there being no fewer than five possibilities : it may be a new subspecies of *B. pales*, a form of subsp. *pales*, a subspecies of *B. graeca*, a form of subsp. *graeca*, or a form of *B. graeca* subsp. *balcanica*. One can only leave these interesting questions to be decided at some future date.

VI. Check List of the Species and Subspecies of the Genus *Boloria*.

1. *B. napaea* (Hoffmsg.)
    - subsp. *napaea* (Hoffmsg.)
        - f. *atroviolacea* Verity
        - f. *atroviridans* Verity
        - f. *frigida* Wrn.
    - subsp. *altaica* (Gr.-Gr.)
        - f. *frigidalis* Wrn.
    - subsp. *nikolajewski* (Heydem.)
    - subsp. *nearctica* Verity
    - subsp. *alaskensis* (Holl.)
    - subsp. *halli* Klots
    - (subsp. ?) *reiffi* Rs.
2. *B. pales* ([Denis & Schiff.])
    - subsp. *pales* ([Denis & Schiff.])
        - (ab. *deflavata* Wagner)
        - f. *palustris* (Frhst.)
        - f. *mixta* Wrn.
    - subsp. *caucasica* (Led.)
    - subsp. *sipora* (Moore)
    - subsp. *nitida* Wrn.
    - subsp. *baralacha* (Moore)
    - subsp. *eupales* (Frhst.)
    - subsp. *palina* (Frhst.)
    - subsp. *palinoides* Rs.
        - (ab. *tatsienlouana* Rs.)
    - subsp. *sifanica* (Gr.-Gr.)
    - subsp. *lucida* (B.-Haas)
    - subsp. *korla* (Frhst.)
        - (ab. *darjana* Seitz)
    - subsp. *generator* (Stg.)
        - f. *juldussica* (Wagner)
    - subsp. *aquilonaris* (Stchl.)
    - subsp. *alethea* (Hemmg.)
    - subsp. *banghaasi* (Seitz)
    - subsp. *pyrenesmiscens* Verity
3. *B. graeca* (Stg.)
    - subsp. *graeca* (Stg.)
    - subsp. *balcanica* (Rbl.)
    - subsp. *brogotarus* (Frhst.)
        - f. *medioitalica* (Trti.)

Unclassified *Boloria* races.

B. species ?
- (? subsp. or f.) *contempta* (Zerny)
- (? subsp. or f.) *neopales* (Nakahara)

Important Synonyms

Of *B. napaea* (Hoffmsg.)
- subsp. *dirphya* (Hoffmsg.)
- subsp. *isis* (Hb.)
- subsp. *isisoides* (Heydem.)

Of *B. pales* ([Denis & Schiff.])
- subsp. *arsilache* (Esp.)
- subsp. *arsilache* (Hb.)
- subsp. *hunzaica* (Tytler)
- subsp. *hypoarsilache* Verity
- var. *lapponica* (Stg.)

Of *B. graeca* (Stg.)
- subsp. *majellensis* (Danhl.)
- subsp. *tendensis* (Higgins)

Of *B.* species ?
- subsp. *sachalinensis* (Mats.)

Note :—If readers miss certain names in the above list, they may feel reasonably sure, especially in the case of names published prior to 1939, that these have been omitted because they only stand for aberrations. In this connection, however, one name must be referred to :—

Brenthis pales arsilache Esp. forma *hannoverana* Füge, 1912, *Z. wiss. Insekten-Biol.* **8 :** 189.

This name was given to a melanic aberration of subsp. *alethea* (i.e. *arsilache* Esp. of Füge). By " forma," Füge obviously had no intention of suggesting that his *hannoverana* was a recurring form, for he starts with the words " Ein stark melanotisches Stück mit schwarzer, bläulich schimmernder Oberseite ", and ends with a reference to " Diese wunderschöne Aberration."

The aberration is a very remarkable one, in that the bluish (or perhaps bluish-purple) gloss, such as occurs so frequently in females of *Boloria napaea,* is only known to appear in two subspecies of *B. pales,* both Asiatic. Very rarely I have noted a suggestion of a purple sheen on a female of subsp. *aquilonaris,* but never anything approaching that suggested by Füge's description and figure. The latter is very similar to one of the most extreme examples of *B. napaea* ♀ form *atroviolacea,* and without seeing the specimen one could not say if it might not be the latter. We can, however, accept Füge's identification of the specimen, for he had the knowledge of the local race with which it was found. Of course the deep black suffusion that spreads over the entire upperside probably increases the purple gloss, and this gloss would not appear so strong on an otherwise normally marked female. All the same, such a specimen must be extremely rare in any European race of *B. pales.*

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EXPLANATION OF PLATES 1–46.

The following points should be noted.

(1) The magnification of the photographs of the genitalia is indicated in the legend of each plate.
(2) All photographs of the butterflies are exactly life-size.
(3) When the upperside and underside *of the same specimen* are illustrated, this is always stated to be so in the legend; if no mention is made of the fact, the figures are taken from different specimens.

All photographs are by the Author.

PLATE 1.

Male armatures, all × 18.

Argynnis paphia.

FIG. 1. Periphallic organs and phallus (ventral view). Craigavad, Co. Down. (Same specimen as fig. 2.)
2. Tegumen and uncus (lateral view). (Same specimen as fig. 1.)
3. Tegumen and uncus (lateral view). Digne, Basses Alpes.

PLATE 2.

Male armatures, all × 18.

Pandoriana pandora.

FIG. 4. Periphallic organs and phallus (ventral view). Tattone, Corsica. (Same specimen as fig. 6.)
5. Tegumen and uncus (lateral view). Corte, Corsica.
6. Uncus (lateral view). (Same specimen as fig. 4.)
7. Uncus (lateral view). Tattone, Corsica.

PLATE 3.

Male armatures, all × 18.

Argyronome laodice.

FIG. 8. Periphallic organs and phallus (ventral view). Askold Island, Siberia.
9. Tegumen and uncus (lateral view). Foochow.

PLATE 4.

Male armatures, × 18 unless otherwise marked.

Issoria lathonia.

FIG. 10. Genitalia (lateral view, left clasper removed). Digne, Basses Alpes.
11. Uncus × 50 (ventral view). Martigny, Valais.
12. Tegumen, uncus and gnathus, × 50 (lateral view). Kaiserstuhl, Baden.

PLATE 5.

Male armatures, all × 18.

Fabriciana niobe.

FIG. 13. Periphallic organs and phallus (ventral view). Fusio, Ticino.

Fabriciana adippe.

FIG. 14. Periphallic organs and phallus (ventral view). Seis, Dolomites. (Same specimen as fig. 17, pl. 6.)

PLATE 6.

Male armatures, all × 18.

Fabriciana niobe f. *eris.*

FIG. 15. Tegumen, uncus and gnathal plates (lateral view). Meix, Valais.

Fabriciana elisa.

FIG. 16. Tegumen, uncus and gnathal plates (lateral view). Tattone, Corsica. (Same specimen as fig. 21, pl. 7.)

Fabriciana adippe.

FIG. 17. Tegumen, uncus and gnathal plates (lateral view). Seis, Dolomites. (Same specimen as fig. 14, pl. 5.)
18. Gnathal plates (dorsal view). Freiburg, Baden.

Mesoacidalia charlotta (= *aglaja* (L.)).

FIG. 19. Tegumen and uncus (lateral view). Ferpècle, Valais. (Same specimen as fig. 22, pl. 7.)
20. Tegumen, uncus and gnathal plates (lateral view). Mallnitz, Carinthia. (Same specimen as fig. 23, pl. 7.)

PLATE 7.

Male armatures, all × 18.

Fabriciana elisa.

FIG. 21. Periphallic organs and phallus (ventral view). Tattone, Corsica. (Same specimen as fig. 16, pl. 6.)

Mesoacidalia charlotta (= *aglaja* (L.)).

FIG. 22. Phallobase (ventral view). Ferpècle, Valais. (Same specimen as fig. 19, pl. 6.)
23. Periphallic organs and phallus (central view). Mallnitz, Carinthia. (Same specimen as fig. 20, pl. 6.)

Plate 8.

Male armatures, all × 18.

Brenthis hecate.

Fig. 24. Genitalia (complete, ventral view). St. Zackarie, Provence. (Same specimen as fig. 26, pl. 9.)

Brenthis daphne.

Fig. 25. Genitalia (complete, ventral view). Seis, Dolomites.

Plate 9.

Male armatures, × 18 unless otherwise marked.

Brenthis hecate.

Fig. 26. Uncus × 50 (ventral view). St. Zackarie, Provence. (Same specimen as fig. 24, pl. 8.)

Brenthis daphne.

Fig. 27. Uncus × 50 (ventral view). Martigny, Valais.

Brenthis ino.

Fig. 28. Periphallic organs and phallus (ventral view). Villeneuve, Vaud. (Same specimen as fig. 30.)
29. Uncus × 50 (lateral view). Mt. Cubli, Vaud.
30. Uncus × 50 (ventral view). (Same specimen as fig. 28.)

Plate 10.

Male armatures, × 18 unless otherwise marked.

Clossiana titania.

Fig. 31. Genitalia (lateral view, left clasper removed). Mallnitz, Carinthia.
32. Uncus × 50 (ventral view). Pontresina, Grisons. (Same specimen as fig. 33.)
33. Aedeagus × 37 (lateral view). (Same specimen as fig. 32.)
34. Aedeagus and phallobasic processes × 37 (ventral view). Fusio, Ticino.

Plate 11.

Male armatures, × 18 unless otherwise marked.

Clossiana euphrosyne.

Fig. 35. Periphallic organs and phallus (ventral view). Kandersteg, Bern. (Same specimen as fig. 36.)
36. Tegumen and uncus (lateral view). (Same specimen as fig. 35.)

Clossiana thore.

Fig. 37. Periphallic organs and phallus (ventral view). Karer See, Dolomites. (Same specimen as fig. 39.)
38. Uncus × 50 (ventral view). Tschitta Pass, Grisons.
39. Tegumen and uncus (lateral view). (Same specimen as fig. 37.)

Clossiana dia.

Fig. 40. Genitalia (lateral view, left clasper removed). Salquenen, Valais.

PLATE 12.

Male armatures, × 18 unless otherwise marked.

Clossiana selene.

FIG. 41. Genitalia (lateral view, left clasper removed). Reazzino, Ticino.
42. Uncus × 50 (ventral view). Reazzino, Ticino.

Proclossiana eunomia.

FIG. 43. Genitalia (complete, ventral view). Hockai, Belgium.
44. Tegumen and uncus (lateral view). Hockai, Belgium.

PLATE 13.

Male armatures, all × 18.

Boloria napaea subsp. *napaea.*

FIG. 45. Genitalia (lateral view, left clasper removed). Mallnitz, Carinthia. (Specimen shown figs. 148, 149, pl. 30.)
46. Periphallic organs and phallus (ventral view). "Latemar Meadow," Karer Pass, Dolomites. (Specimen shown fig. 150, pl. 30.)
47. Periphallic organs and phallus (ventral view). Val Minor, Grisons.
48. Periphallic organs and phallus (ventral view). Val Minor, Grisons.
49. Periphallic organs and phallus (ventral view). Lenzerheide, Grisons.
50. Periphallic organs and phallus (ventral view). Val Minor, Grisons.

PLATE 14.

Male armatures, all × 18.

Boloria napaea subsp. *napaea.*

FIG. 51. Periphallic organs and phallus (ventral view). Heu Tal, Grisons.

Subsp. *napaea* f. *frigida.*

FIG. 52. Periphallic organs and phallus (ventral view). Abisko, N. Sweden. (Specimen shown fig. 171, pl. 32.)

Subsp. *napaea.*

FIG. 53. Periphallic organs and phallus (ventral view). Dent du-Midi, Valais.

Subsp. *napaea* f. *frigida.*

FIG. 54. Periphallic organs and phallus (central view). Abisko, N. Sweden. (Specimen shown fig. 170, pl. 32.)
55. Periphallic organs and phallus (ventral view). Maalselven, N. Norway. (Specimen shown figs. 172, 173, pl. 32.)
56. Periphallic organs and phallus (ventral view). Maalselven, N. Norway. (Specimen shown fig. 174, pl. 32.)

PLATE 15.

Male armatures, all × 18.

Boloria napaea subsp. *napaea* f. *frigida.*

FIG. 57. Periphallic organs and phallus (ventral view). Maalselven, N. Norway.
58. Periphallic organs and phallus (ventral view). Rundhaug, N. Norway.
59. Periphallic organs and phallus (ventral view). Abisko, N. Sweden. (Specimen shown figs. 168, 169, pl. 32.)

Subsp. *napaea.*

FIG. 60. Periphallic organs and phallus (ventral view). Damaas, Dovre Fjeld, Norway.

Subsp. *nearctica.*

FIG. 61. Periphallic organs and phallus (ventral view). Arctic America, 114° 30′ W. 67° 40′ N. (Same specimen as fig. 64, pl. 16.)

62. Periphallic organs and phallus (ventral view). Arctic America, 114° 30′ W. 67° 40′ N. (Specimen shown figs. 188, 189, pl. 34.)

PLATE 16.

Male armatures, all × 18.

Boloria napaea subsp. *napaea.*

FIG. 63. Genitalia (complete, ventral view). Anthemoz, Valais.

Subsp. *nearctica.*

FIG. 64. Tegumen and uncus (lateral view). Arctic America, 114° 30′ W. 67° 40′ N. (Same specimen as fig. 61, pl. 15.)

Subsp. *altaica* f. *frigidalis.*

FIG. 65. Tegumen and uncus (lateral view). Arasan, Altai.

Subsp. *altaica.*

FIG. 66. Periphallic organs and phallus (ventral view). Irkut. (Specimen shown figs. 180, 181, pl. 33.)

Subsp. *nikolajewski.*

FIG. 67. Periphallic organs and phallus (ventral view). Jakutsk. (Same specimen as fig. 69; specimen shown figs. 186, 187, pl. 33.)

Subsp. *napaea.*

FIG. 68. Periphallic organs and phallus (ventral view). Anthemoz, Valais.

Subsp. *nikolajewski.*

FIG. 69. Tegumen and uncus (lateral view). (Same specimen as fig. 67.)

PLATE 17.

Male armatures, all × 18.

Boloria napaea subsp. *napaea.*

FIG. 70. Periphallic organs and phallus (ventral view). "Latemar Meadow," Karer Pass, Dolomites. (Specimen shown fig. 151, pl. 30.)

Boloria pales subsp. *pales.*

FIG. 71. Periphallic organs and phallus (ventral view). "Latemar Meadow," Karer Pass, Dolomites. (Specimen shown fig. 207, pl. 35.)

Boloria napaea subsp. *napaea.*

FIG. 72. Periphallic organs and phallus (ventral view). Val Minor, Grisons.

Boloria pales subsp. *pales.*

FIG. 73. Periphallic organs and phallus (ventral view). Val Roseg, Grisons.

Boloria napaea subsp. *napaea.*

FIG. 74. Periphallic organs and phallus (ventral view). Morteratsch, Grisons. (Specimen shown fig. 152, pl. 30.)

Boloria pales subsp. *pales.*

FIG. 75. Left clasper (lateral view), and vinculum and saccus (ventral view). Morteratsch, Grisons. (Specimen shown fig. 211, pl. 36.)

PLATE 18.

Male armatures, all × 18.

Boloria napaea subsp. *altaica*.

FIG. 76. Genitalia (complete, ventral view). Tchuja Mountains, S.E. Altai.

Subsp. *altaica* f. *frigidalis*.

FIG. 77. Periphallic organs and phallus (ventral view). Tchuja Mountains, S.E. Altai. (Specimen shown figs. 184, 185, pl. 33.)

Boloria pales subsp. *korla*.

FIG. 78. Periphallic organs and phallus (ventral view). E. Turkestan.

Subsp. *generator*.

FIG. 79. Periphallic organs and phallus (ventral view). Margilan, Tian Shan.

Subsp. *sipora*.

FIG. 80. Periphallic organs and phallus (ventral view). Kulu, Punjab. (Same specimen as fig. 103, pl. 22; specimen shown figs. 226, 227, pl. 37.)

PLATE 19.

Male armatures, all × 18.

Boloria pales subsp. *pales*.

FIG. 81. Genitalia (lateral view, left clasper removed). Mallnitz, Carinthia.
82. Periphallic organs and phallus (ventral view). Tatra.
83. Periphallic organs and phallus (ventral view). Mallnitz, Carinthia.
84. Periphallic organs and phallus (ventral view). Mallnitz, Carinthia.
85. Periphallic organs and phallus (ventral view). "Latemar Meadow," Karer Pass, Dolomites. (Specimen shown fig. 206, pl. 35.)
86. Periphallic organs and phallus (ventral view). Karer Pass, Dolomites.

PLATE 20.

Male armatures, all × 18.

Boloria pales subsp. *pales*.

FIG. 87. Periphallic organs and phallus (ventral view). Nebelhorn, Allgauer Alps.
88. Periphallic organs and phallus (ventral view). Nebelhorn, Allgauer Alps.
89. Periphallic organs and phallus (ventral view). Val Minor, Grisons. (Specimen shown fig. 212, pl. 36.)
90. Periphallic organs and phallus (ventral view). Campolunga Pass, Ticino.
91. Periphallic organs and phallobase (ventral view). Niesen, Bern.
92. Periphallic organs and phallus (ventral view). Grammont, Valais.

PLATE 21.

Male armatures, all × 18.

Boloria pales subsp. *pales*.

FIG. 93. Periphallic organs and phallus (ventral view). Kandersteg Bern.
94. Periphallic organs and phallus (ventral view). Kandersteg, Bern.
95. Periphallic organs and phallus (ventral view). Kandersteg, Bern.
96. Periphallic organs and phallus (ventral view). Kandersteg, Bern.

Subsp. *pales* f. *palustris*.

FIG. 97. Periphallic organs and phallus (ventral view). Zinal, Valais.
98. Periphallic organs and phallus (ventral view). Zinal, Valais. (Specimen shown fig. 218, pl. 37.)

PLATE 22.

Male armatures, × 18 unless otherwise marked.

Boloria pales subsp. *caucasica.*

FIG. 99. Periphallic organs and phallus (ventral view). Locality uncertain.

Subsp. *sipora.*

FIG. 100. Periphallic organs and phallus (ventral view). Gulmarg, Kashmir.

Subsp. *nitida.*

FIG. 101. Periphallic organs and phallus (ventral view). Stakspi Pass, Kashmir.

Subsp. *baralacha.*

FIG. 102. Periphallic organs and phallus (ventral view). Koksar, E. Punjab.

Subsp. *sipora.*

FIG. 103. Uncus, × 50 (ventral view). Kulu, E. Punjab. (Same specimen as fig. 80, pl. 18.)

Subsp. *palina.*

FIG. 104. Uncus, × 50 (ventral view). Tusk, S. Tibet. (Same specimen as fig. 105, pl. 23.)

PLATE 23.

Male armatures, all × 18.

Boloria pales subsp. *palina.*

FIG. 105. Periphallic organs and phallobase (ventral view). Tusk, S. Tibet. (Same specimen as fig. 104, pl. 22.)

Subsp. *sifanica.*

FIG. 106. Genitalia (complete, ventral view). Amdo District, central Tibet. (Specimen shown figs. 252, 253, pl. 40.)
107. Periphallic organs and phallus (ventral view). Amdo District, central Tibet.
108. Periphallic organs and phallus (ventral view). Hou-Kow, Tibet. (Specimen shown figs. 256, 257, pl. 40.)

Subsp. *palina.*

FIG. 109. Periphallic organs and phallus (ventral view). Ta-tsien-lu, Szechwan.
110. Periphallic organs and phallobase (ventral view). Siao-lu, Szechwan.

PLATE 24.

Male armatures, all × 18.

Boloria pales subsp. *palinoides.*

FIG. 111. Periphallic organs and phallus (ventral view). Sung-pan-ting, Szechwan.

Subsp. *korla.*

FIG. 112. Genitalia (complete, ventral view). E. Turkestan.
113. Periphallic organs and phallus (central view). E. Turkestan. (Specimen shown figs. 258, 259, pl. 41.)

Subsp. *generator.*

FIG. 114. Periphallic organs and phallus (ventral view). Tura, Tian Shan.
115. Periphallic organs and phallus (ventral view). Skoro-La. (Same specimen as fig. 116; specimen shown figs. 268, 269, pl. 42.)
116. Tegumen and uncus (lateral view). (Same specimen as fig. 115).

Subsp. *alethea.*

FIG. 117. Tegumen and uncus (lateral view). Harz Mountains.

PLATE 25.

Male armatures, all × 18.

Boloria pales subsp. *aquilonaris.*

FIG. 118. Periphallic organs and phallus (ventral view). Abisko, N. Sweden. (Specimen shown fig. 272, pl. 42.)
119. Periphallic organs and phallus (ventral view). Saltdalen, N. Norway.
120. Periphallic organs and phallus (ventral view). Damaas, Dovre Fjeld, Norway. (Specimen shown figs. 276, 277, pl. 42.)
121. Periphallic organs and phallus (ventral view). Mouhijarvi, Finland.
122. Periphallic organs and phallobase (ventral view). Mouhijarvi, Finland.
123. Periphallic organs and phallus (ventral view). Mouhijarvi, Finland.

PLATE 26.

Male armatures, all × 18.

Boloria pales subsp. *aquilonaris.*

FIG. 124. Periphallic organs and phallus (ventral view). St. Petersburg. (Specimen shown fig. 279, pl. 43.)
125. Periphallic organs and phallus (ventral view). Bashkaus, Altai.
126. Periphallic organs and phallus (ventral view). Hinterzarten, Black Forest.
127. Periphallic organs and phallus (ventral view). Hinterzarten, Black Forest.
128. Periphallic organs and phallus (ventral view). Campfer, Engadine.

Subsp. *alethea.*

FIG. 129. Periphallic organs and phallus (ventral view). Aschau, S. Bavaria.

PLATE 27.

Male armatures, all × 18.

Boloria pales subsp. *alethea.*

FIG. 130. Periphallic organs and phallus (ventral view). Harz Mountains.
131. Periphallic organs and phallus (ventral view). Harz Mountains.
132. Periphallic organs and phallus (ventral view). Harz Mountains.

Subsp. *banghaasi.*

FIG. 133. Periphallic organs and phallus (ventral view). Kentei Mountains. (Specimen shown figs. 294, 295, pl. 44.)

Subsp. *pyrenesmiscens.*

FIG. 134. Periphallic organs and phallus (ventral view). Pajares, Cantabrian Mountains.
135. Periphallic organs and phallus (ventral view). Picos de Europa, Cantabrian Mountains.

PLATE 28.

Male armatures, all × 18.

Boloria pales subsp. *pyrenesmiscens*.

FIG. 136. Periphallic organs and phallus (ventral view). Gavarnie, Hautes Pyrénées.
137. Periphallic organs and phallus (ventral view). Gavarnie, Hautes Pyrénées.
138. Periphallic organs and phallus (ventral view). Gavarnie, Hautes Pyrénées.
139. Periphallic organs and phallus (ventral view). Gavarnie, Hautes Pyrénées.
140. Periphallic organs and phallus (ventral view). Gavarnie, Hautes Pyrénées.
141. Periphallic organs and phallus (ventral view). Eaux Bonnes, Basses Pyrénées.

PLATE 29.

Male armatures, all × 18.

Boloria graeca subsp. *graeca*.

FIG. 142. Periphallic organs and phallus (ventral view). Greece.
143. Periphallic organs and phallus (ventral view). Greece.

Subsp. *balcanica*.

FIG. 144. Periphallic organs and phallus (ventral view). Bosnia.
145. Periphallic organs and phallus (ventral view). Rilo Dagh, Bulgaria.

Subsp. *brogotarus*.

FIG. 146. Periphallic organs and phallus (ventral view). Col di Tenda, Maritime Alps.
147. Periphallic organs and phallus (ventral view). Col di Tenda, Maritime Alps.

PLATE 30.

Boloria napaea subsp. *napaea*.

FIG. 148. ♂, Jamnig Alp, Mallnitz, Carinthia; 5500–6100 ft. **(Genitalia fig. 45.)**
149. ♂, underside of fig. 148.
150. ♂, "Latemar Meadow," Karer Pass, Dolomites; 6300 ft. **(Genitalia fig. 46.)**
151. ♂, underside, "Latemar Meadow," Karer Pass, Dolomites; 6300 ft. **(Genitalia fig. 70.)**
152. ♂, Surovas to Morteratsch, Grisons; 6000–6200 ft. **(Genitalia fig. 74.)**
153. ♀, "Latemar Meadow," Karer Pass, Dolomites; 6300 ft.
154. ♂, Surovas to Morteratsch, Grisons; 6000–6200 ft.
155. ♀, Surovas to Morteratsch, Grisons; 6000–6200 ft.
156. ♂ (aberration); Surovas to Morteratsch, Grisons; 6000–6200 ft.
157. ♂ (aberration); Val. Minor, Grisons; 7200–7500 ft.

PLATE 31.

Boloria napaea subsp. *napaea*.

FIG. 158. ♀, Anthemoz, Valais.
159. ♀ (aberration); Val Minor, Grisons; 7200–7500 ft.
160. ♀, Piz Albris (eastern slopes), Grisons; 7600 ft.

FIG. 161. ♀, underside of fig. 160.
162. ♀, Lenzerheide, Grisons; 5200 ft.
163. ♀, underside of fig. 162.
164. ♂, Damaas, Dovre Fjeld, Norway.
165. ♂, underside of fig. 164.
166. ♀, Damaas, Dovre Fjeld, Norway.
167. ♀, underside of fig. 166.

PLATE 32.

Boloria napaea subsp. *napaea* f. *frigida.*

FIG. 168. ♂, Abisko, N. Sweden. **(Genitalia fig. 59.)**
169. ♂, underside of fig. 168.
170. ♂, Abisko, N. Sweden. **(Genitalia fig. 54.)**
171. ♂, underside, Abisko, N. Sweden. **(Genitalia fig. 52.)**
172. ♂, Maalselven, N. Norway. **Type.** **(Genitalia fig. 55.)**
173. ♂, underside of fig. 172.
174. ♂, Maalselven, N. Norway. **(Genitalia fig. 56.)** **Paratype.**
175. ♀, Abisko, N. Sweden.
176. ♀, Maalselven, N. Nowway. **Paratype.**
177. ♀, underside of fig. 176.

PLATE 33.

Boloria napaea subsp. *altaica.*

FIG. 178. ♂, Bashkaus, S.E. Altai.
179. ♂, underside of fig. 178.
180. ♂, Irkut. **(Genitalia fig. 66.)**
181. ♂, underside of fig. 180.
182. ♀, Arasan, Altai; 6000 ft.
183. ♀, underside, Irkut.

Subsp. *altaica* f. *frigidalis.*

FIG. 184. ♂, Tchuja Mountains, S.E. Altai. Type. **(Genitalia fig. 77.)**
185. ♂, underside of fig. 184.

Subsp. *nikolajewski.*

FIG. 186. ♂, Schigansk, near Jakutsk. **(Genitalia fig. 67.)**
187. ♂, underside of fig. 186.

PLATE 34.

Boloria napaea subsp. *nearctica.*

FIG. 188. ♂, Arctic America, 114° 30′ W., 67° 40′ N. **(Taken by D. H. Hanbury; genitalia fig. 62.)**
189. ♂, underside of fig. 188.
190. ♀, Arctic America, 114° 30′ W., 67° 40′ N. **(Taken by D. H. Hanbury.)**
191. ♀, underside of fig. 190.

Boloria pales subsp. *pales.*

FIG. 192. ♂, Schmecks, Tatra.
193, ♂, underside of fig. 192.
194. ♀, Schmecks, Tatra.
195. ♀, underside, Schmecks, Tatra.
196. ♂, Jamnig Alp, Mallnitz, Carinthia; 5500–6100 ft.
197. ♂, underside, Jamnig Alp, Mallnitz, Carinthia; 5500–6100 ft.

PLATE 35.

Boloria pales subsp. *pales.*

FIG. 198. ♀, Jamnig Alp, Mallnitz, Carinthia; 5500–6100 ft.
199. ♀, underside of fig. 198.
200. ♂, Oberstdorf, Allgauer Alps.
201. ♂, underside of fig. 200.
202. ♂, Nebelhorn, Allgauer Alps; 6000 ft.
203. ♂, underside of fig. 202.
204. ♀, Nebelhorn, Allgauer Alps.
205. ♀, underside of fig. 204.
206. ♂, "Latemar Meadow," Karer Pass, Dolomites; 6300 ft. **(Genitalia fig. 85.)**
207. ♂, underside, "Latemar Meadow," Karer Pass, Dolomites; 6300 ft. **(Genitalia fig. 71.)**

PLATE 36.

Boloria pales subsp. *pales.*

FIG. 208. ♀, "Latemar Meadow," Karer Pass, Dolomites; 6300 ft.
209. ♀, underside, Karer Pass to Ostertag Hut, Dolomites; 5700–7400 ft.
210. ♀, "Latemar Meadow," Karer Pass, Dolomites; 6300 ft.
211. ♂, Surovas to Morteratsch, Grisons; 6000–6200 ft. **(Genitalia fig. 75.)**
212. ♂, Val Minor, Grisons; 7200–7500 ft. **(Genitalia fig. 89.)**
213. ♀, Val Minor, Grisons; 7200–7500 ft.
214. ♂, Niesen, Bernese Alps; 5600–7600 ft.
215. ♂, underside, Niesen, Bernese Alps; 5600–7600 ft.
216. ♀, Niesen Bernese Alps; 5600–7600 ft.
217. ♀, underside, Niesen, Bernese Alps; 5600–7600 ft.

PLATE 37.

Boloria pales subsp. *pales* f. *palustris.*

FIG. 218. ♂, Zinal, Valais. **(Genitalia fig. 98.)**
219. ♂, underside, Zinal, Valais.
220. ♀, Zinal, Valais.
221. ♀, underside, Zinal Valais.

Subsp. *caucasica.*

FIG. 222. ♂, Caucasus.
223. ♂, underside of fig. 222.
224. ♀, Caucasus.
225. ♀, underside of fig. 224.

Subsp. *sipora.*

FIG. 226. ♂, Kulu, E. Punjab; 13,000 ft. **(Genitalia figs. 80 and 103.)**
227. ♂, underside of fig. 226.

PLATE 38.

Boloria pales subsp. *sipora.*

FIG. 228. ♀, Burzil Pass, Kashmir; 12,000 ft.
229. ♀, underside of fig. 228.

Subsp. *nitida.*

Fig. 230. ♂, Chogo Lungma, Baltistan; 13,000 ft. **Holotype.**
231. ♂, underside of fig. 230.
232. ♀, Stakspi Pass, Kashmir; 12,000 ft. **Allotype.**
233. ♀, underside of fig. 232.

Subsp. *baralacha.*

Fig. 234. ♂, Koksar, E. Punjab.
235. ♂, underside of fig. 234.
236. ♀, Bara Lacha, Pass, E. Punjab.
237. ♀, underside of fig. 236.

Plate 39.

Boloria pales subsp. *palina.*

Fig. 238. ♂, Phari, Sikkim; 15,000 ft.
239. ♂, underside of fig. 238.
240. ♀, Tungu, Teesta Vy., Sikkim; 13,000–14,000 ft.
241. ♀, underside of fig. 240.
242. ♂, Ta-tsien-lu, Szechwan. (*From Oberthür coll.*)
243. ♂, underside of fig. 242.
244. ♀, Ta-tsien-lu, Szechwan. (*From Oberthür coll.*)
245. ♀, underside of fig. 244.
246. ♀, Ta-tsien-lu, Szechwan. (*From Oberthür coll.*)
247. ♀, underside of fig. 246.

Plate 40.

Boloria pales subsp. *palinoides.*

Fig. 248. ♂, Ta-tsien-lu, Szechwan. (*From Stötzner expedition.*)
249. ♂, underside of fig. 248.
250. ♀, Sung-pan-ting, Szechwan. (*From Stötzner expedition.*)
251. ♀, underside of fig. 250.

Subsp. *sifanica.*

Fig. 252. ♂, Amdo, central Tibet. **(Genitalia fig. 106.)**
253. ♂, underside of fig. 252.
254. ♀, Amdo, central Tibet.
255. ♀, underside of fig. 254.
256. ♂, Hou-Kow, Tibet. **(Genitalia fig. 108.)**
257. ♂, underside of fig. 256.

Plate 41.

Boloria pales subsp. *korla.*

Fig. 258. ♂, Fort Narine (? Narynsk), Prov. of Semiryechensk, Turkestan. **(Genitalia fig. 113.)**
259. ♂, underside of fig. 258.
260. ♀, Fort Narine, Prov. of Semiryechensk, Turkestan.
261. ♀, underside of fig. 260.
262. ♀, Fort Narine, Prov. of Semiryechensk, Turkestan.
263. ♀, underside of fig. 262.

Subsp. *generator* f. *juldussica.*

Fig. 264. ♂, Hindu-Kush; 15,000 ft.
265. ♂, underside of fig. 264.
266. ♀, Hindu-Kush; 14,000 ft.
267. ♀, underside of fig. 266.

PLATE 42.

Boloria pales subsp. *generator*.

FIG. 268. ♂, Skoro-La; 15,000 ft. **(Genitalia fig. 115.)**
269. ♂, underside of fig. 268.
270. ♀, Skoro-La; 15,000 ft.
271. ♀, underside of fig. 270.

Subsp. *aquilonaris*.

FIG. 272. ♂, Abisko, N. Sweden. **(Genitalia fig. 118.)**
273. ♂, Saltdalen, N. Norway.
274. ♀, Saltdalen, N. Norway.
275. ♀, underside of fig. 274.
276. ♂, Damaas, Dovre Fjeld, Norway. **(Genitalia fig. 120.)**
277. ♂, underside of fig. 276.

PLATE 43.

Boloria pales subsp. *aquilonaris*.

FIG. 278. ♂, underside; Mouhijarvi, Finland.
279. ♂, underside; St. Petersburg. **(Genitalia fig. 124.)**
280. ♀, St. Petersburg.
281. ♀, underside of fig. 280.

Subsp. *alethea*.

FIG 282. ♂, N. Germany.
283. ♂, underside of fig. 282.
284. ♀, N. Germany.
285. ♀, underside of fig. 284.
286. ♂, Harz Mountains.
287. ♂, underside; Harz Mountains.

PLATE 44.

Boloria pales subsp. *alethea*.

FIG. 288. ♀, Harz Mountains.
289. ♀, underside; Harz Mountains.
290. ♂, Schliersee, S. Bavaria; 2500 ft.
291. ♂, underside of fig. 290.
292. ♀, Schliersee, S. Bavaria.
293. ♀, underside of fig. 292.

Subsp. *banghaasi*.

FIG. 294. ♂, Kentei Mountains. **(Genitalia fig. 133.)**
295. ♂, underside of fig. 294.

Subsp. *pyrenesmiscens*.

FIG. 296. ♂, Espinama, Picos de Europa, Cantabrian Mountains.
297. ♂, underside of fig. 296.

PLATE 45.

Boloria pales subsp. *pyrenesmiscens*.

G. 298. ♂, Pajares, Cantabrian Mountains.
299. ♂, underside of fig. 298.
300. ♀, Pajares, Cantabrian Mountains.
301. ♀, underside of fig. 300.

Boloria graeca subsp. *graeca.*

Fig. 302. ♂, Greece.
303. ♂, underside of fig. 302.
304. ♀, Greece.
305. ♀, underside of fig. 304.

Boloria pales subsp. *pales.*

Fig. 306. ♂, Rilo Dagh, S.W. Bulgaria; 5000 ft. (*Taken by Elwes*, 4 *July*, 1899.)
307. ♂, underside of fig. 306.

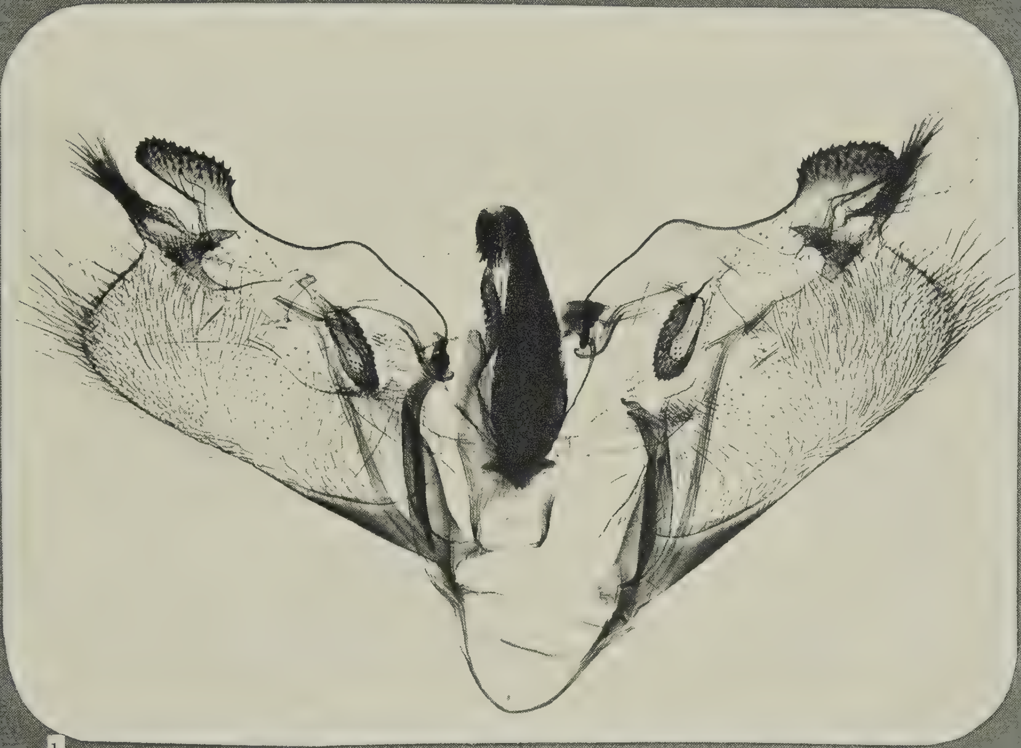
Plate 46.

Boloria graeca subsp. *balcanica.*

Fig. 308. ♂, Rilo Dagh, S.W. Bulgaria; 5000 ft. (*Taken by Elwes*, 30 *June*, 1899.)
309. ♂, underside of fig. 308.
310. ♀, Rilo Dagh, S.W. Bulgaria; 6000 ft.
311. ♂, underside of fig. 310.
312. ♀, Prenj, Bosnia; 5000 ft.
313. ♀, underside of fig. 312.

Subsp. *brogotarus.*

Fig. 314. ♂, Col di Tenda, Maritime Alps. (**Paratype** of *tendensis* Higgins.)
315. ♂, underside of fig. 314.
316. ♀, Col di Tenda, Maritime Alps. (**Paratype** of *tendensis* Higgins.)
317. ♀, underside of fig. 316.



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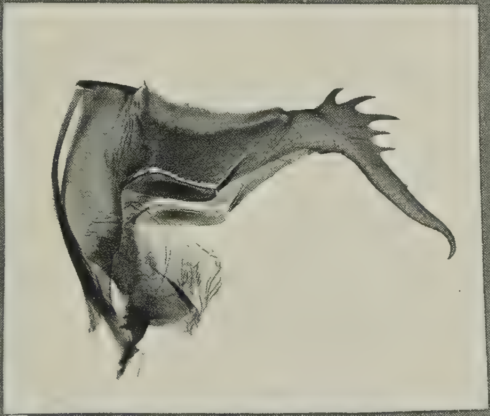

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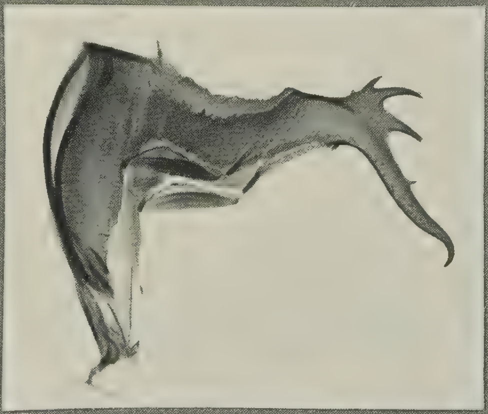

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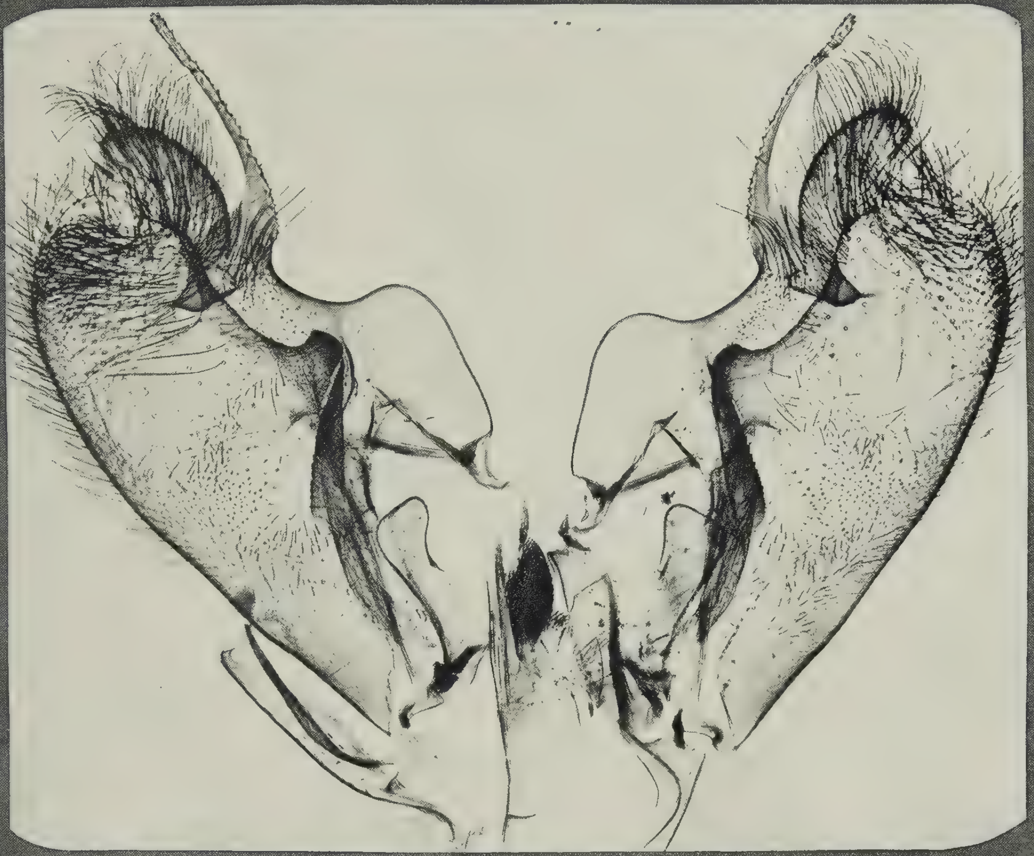

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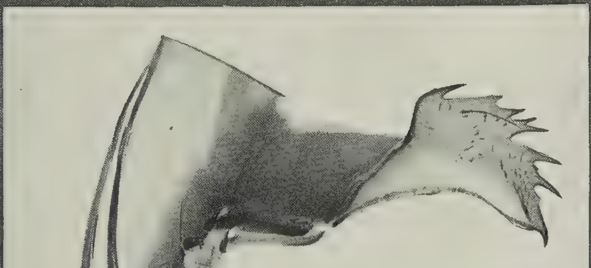

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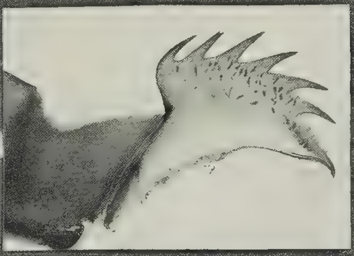

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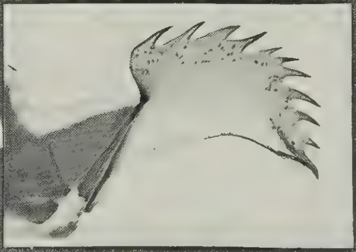

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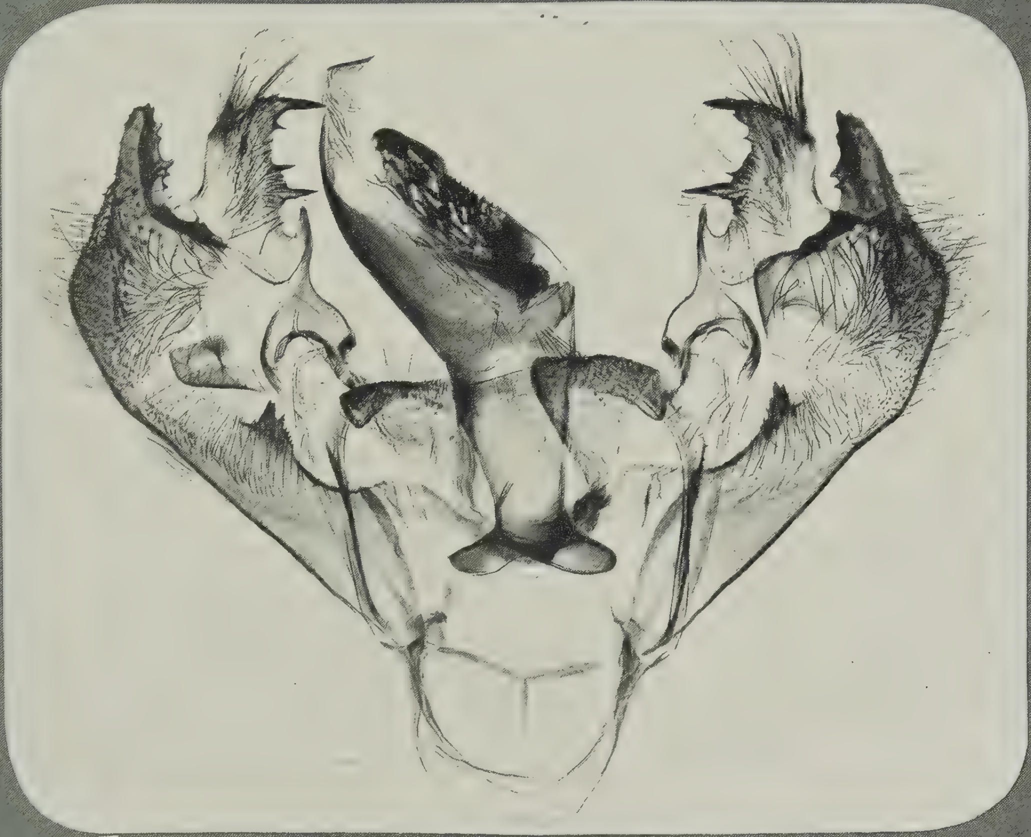

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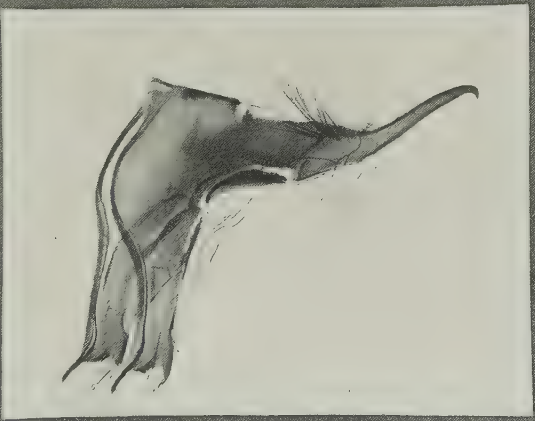

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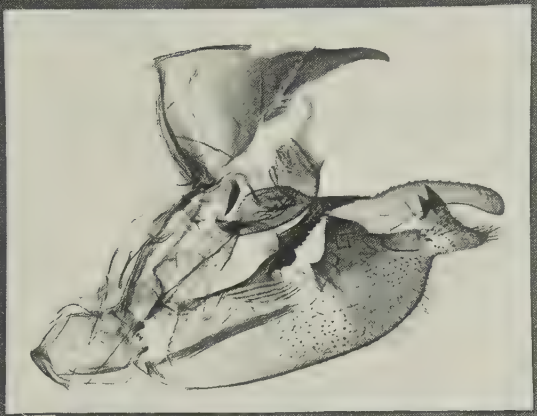

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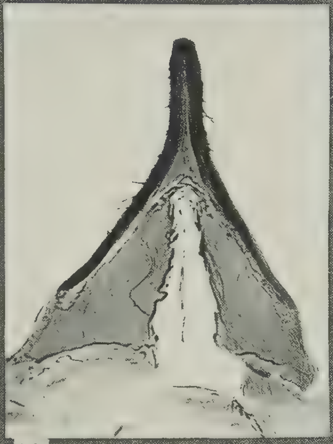

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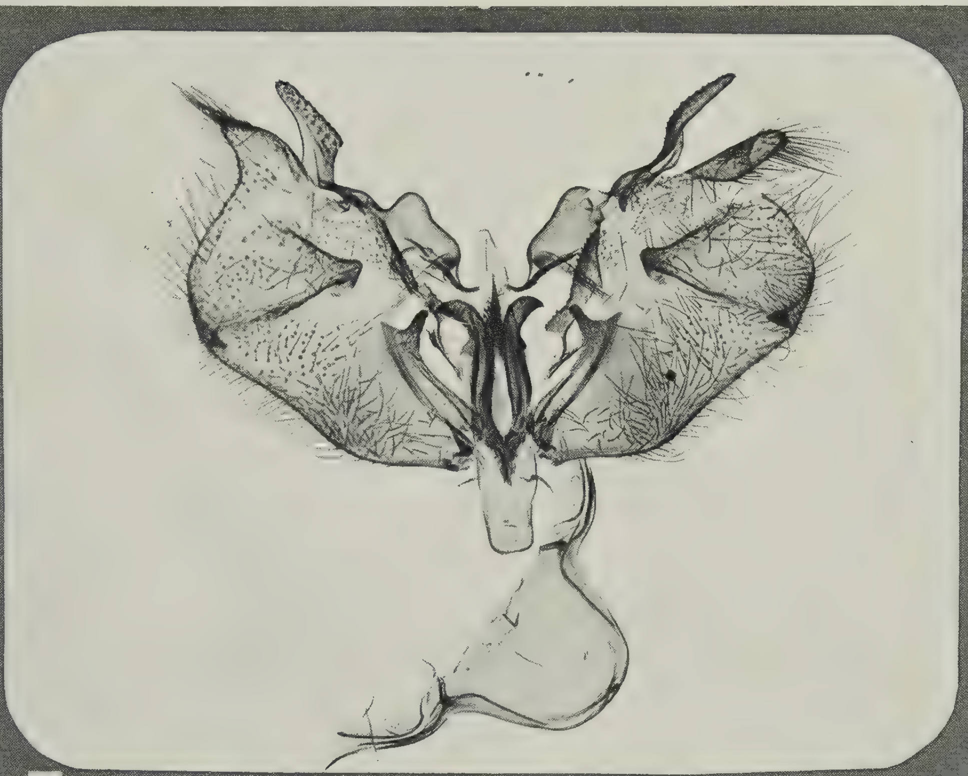

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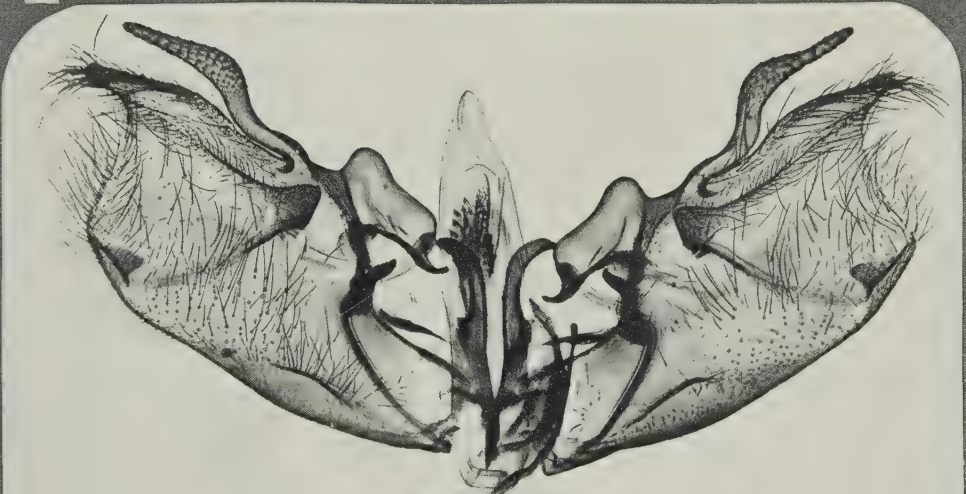

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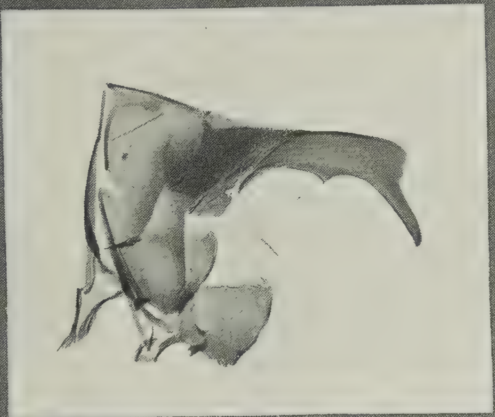
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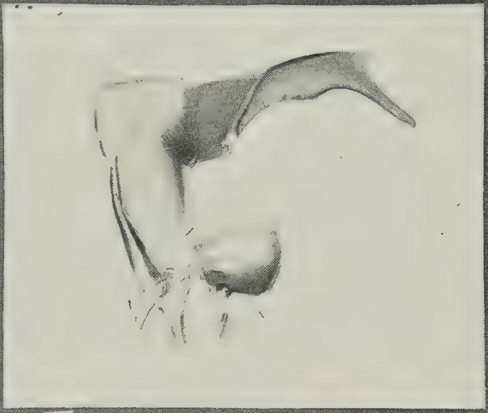
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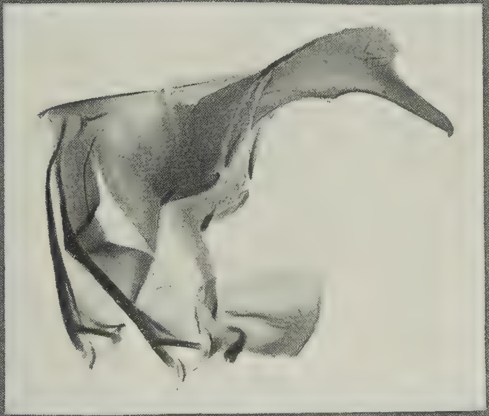
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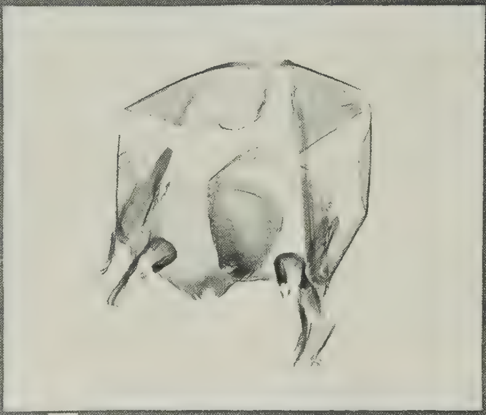
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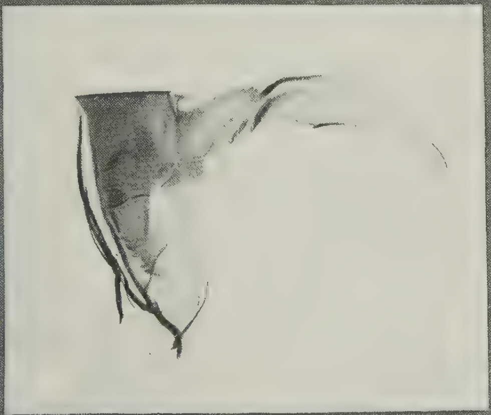
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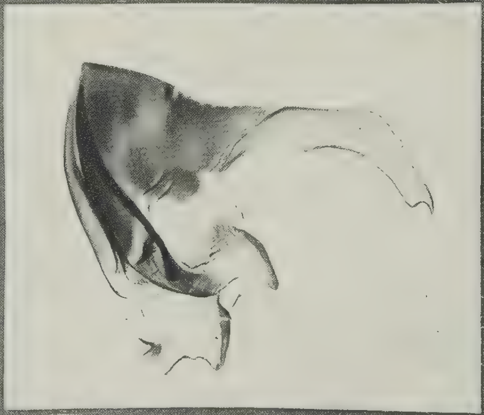
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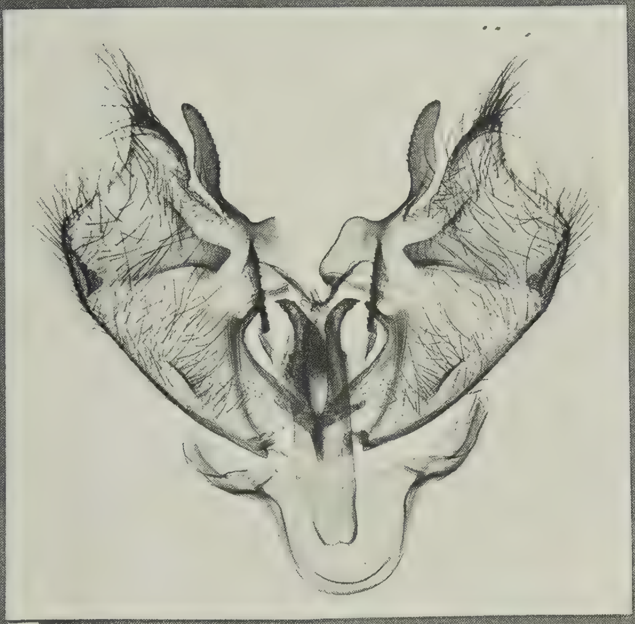
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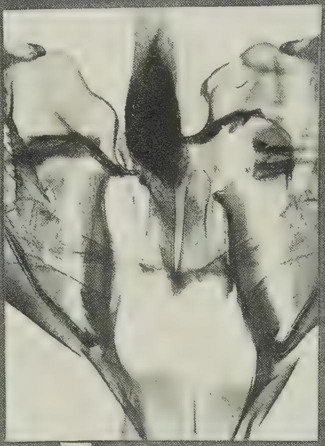
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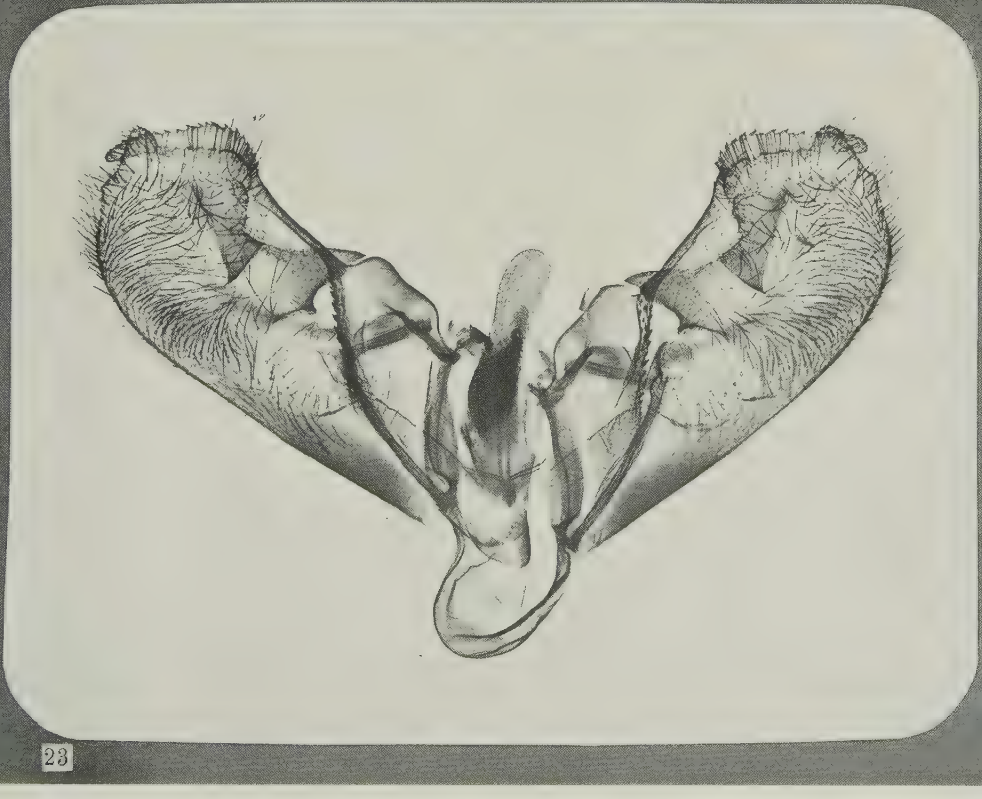
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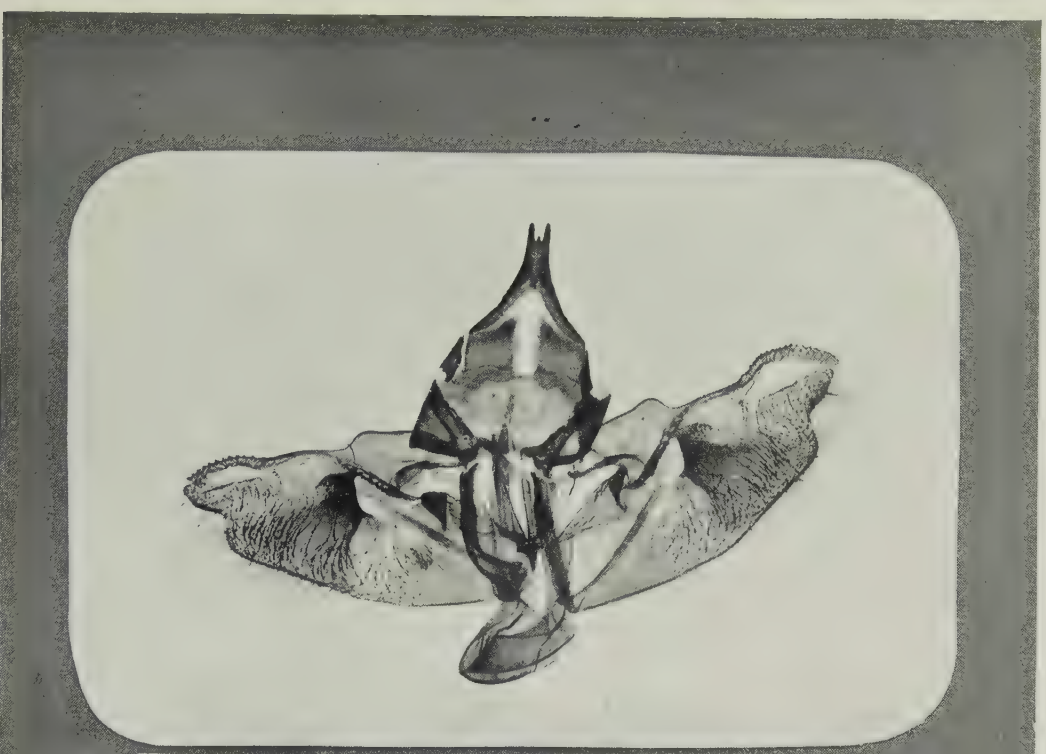

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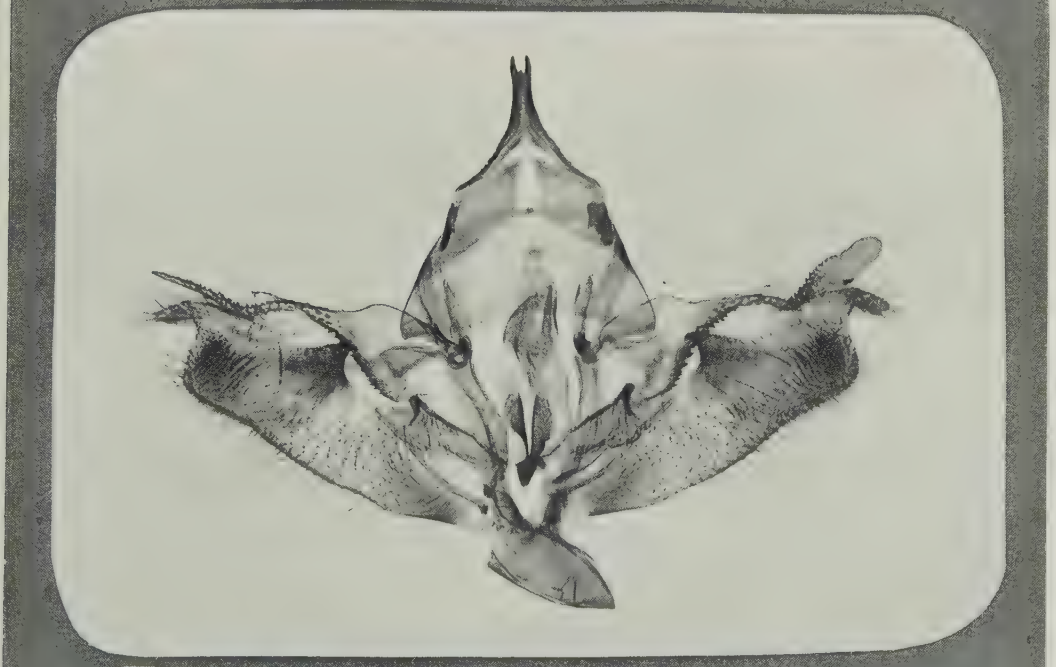

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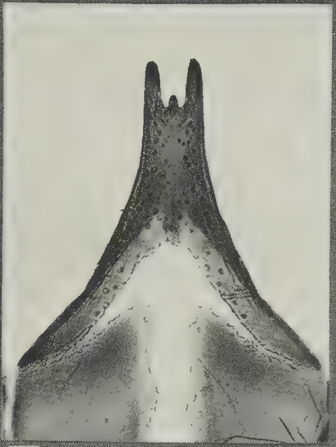
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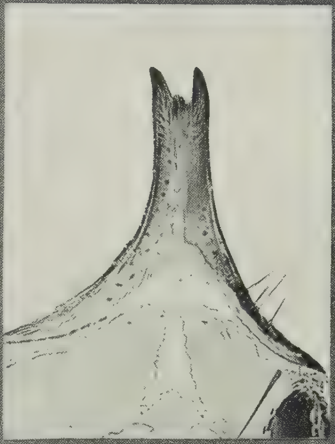
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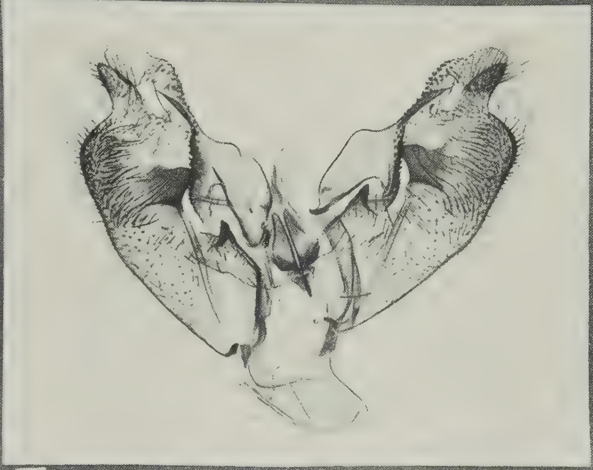
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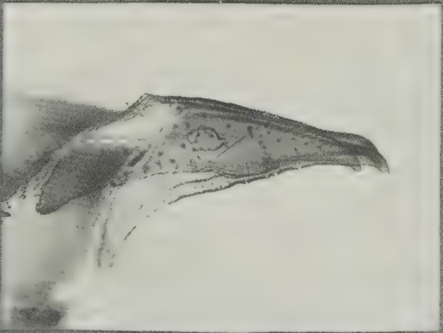
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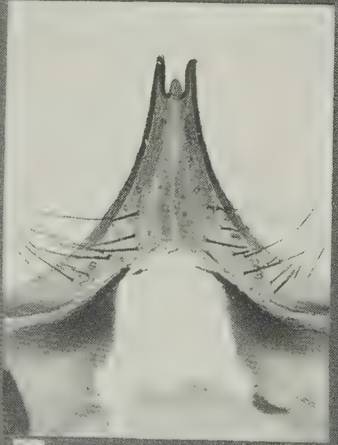
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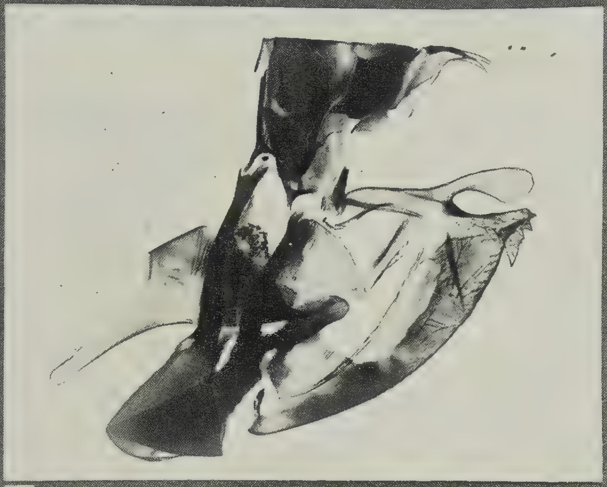

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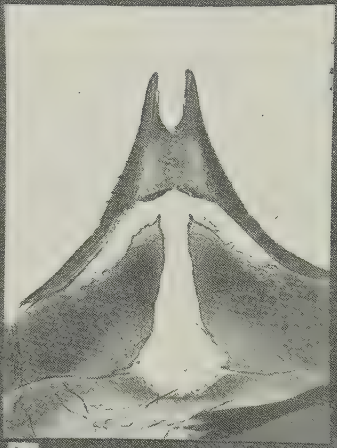

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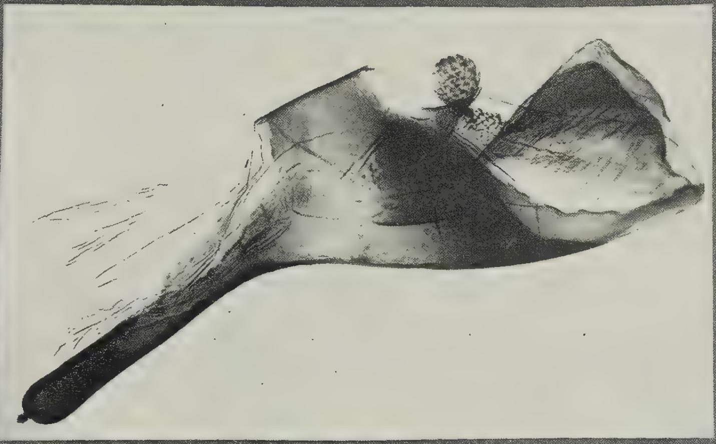

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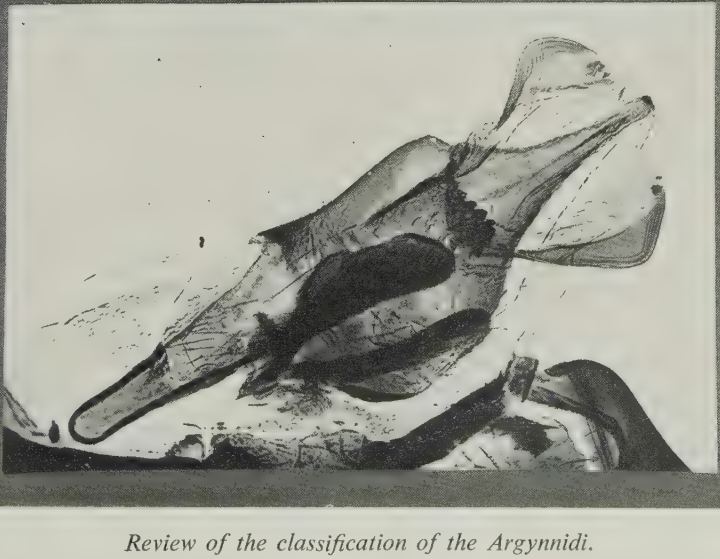

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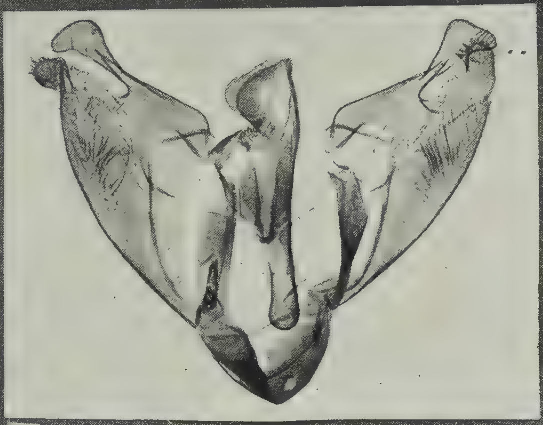

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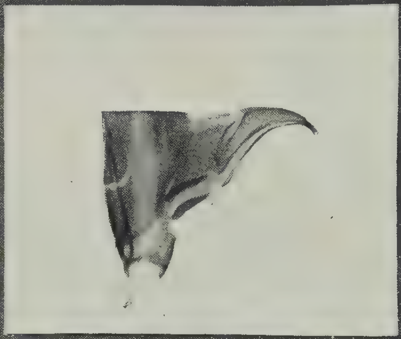

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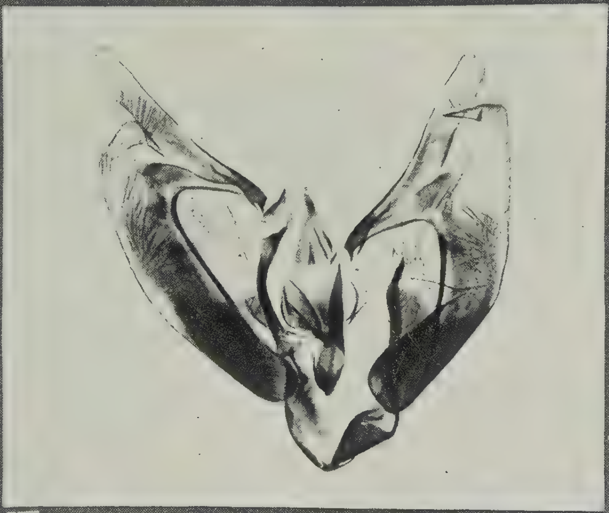

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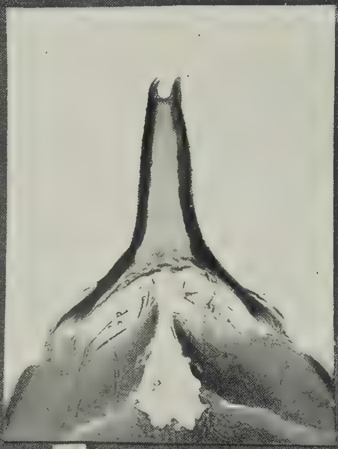

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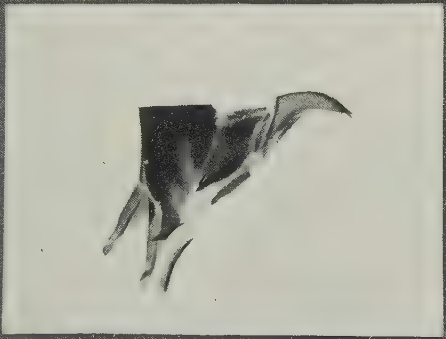

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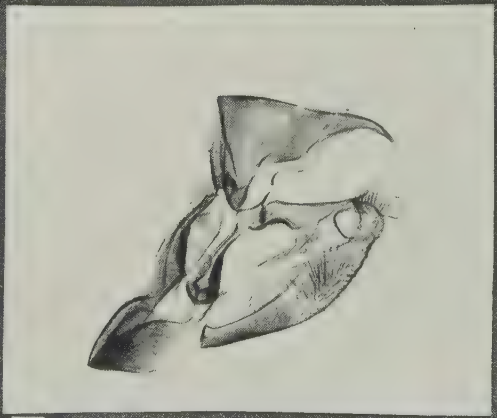

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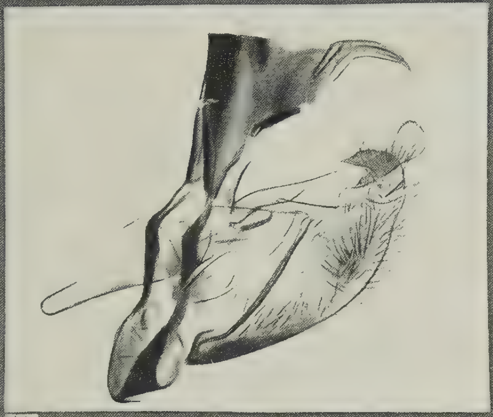

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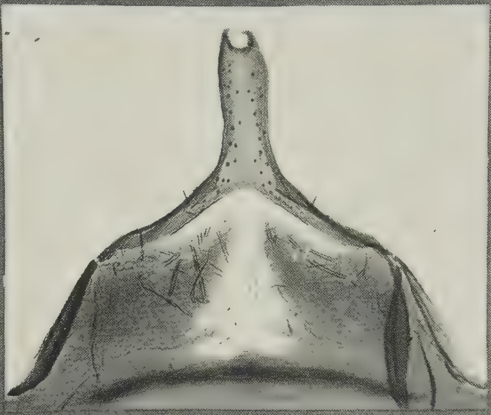

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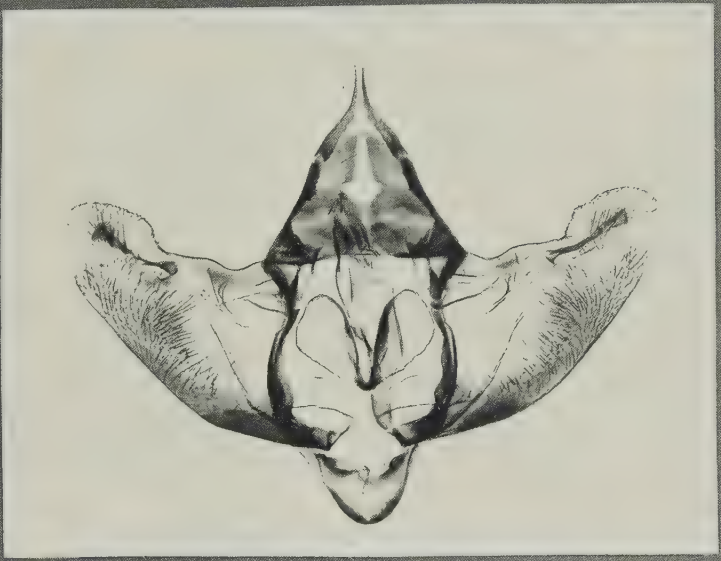

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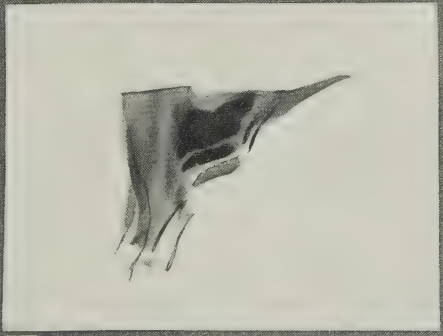

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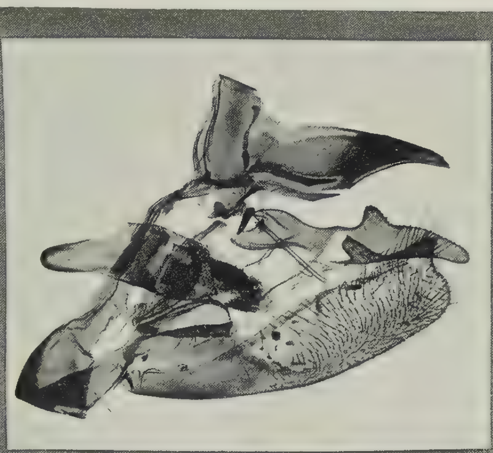
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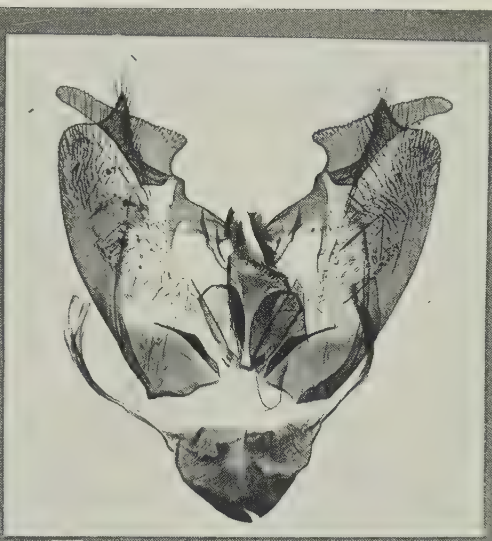
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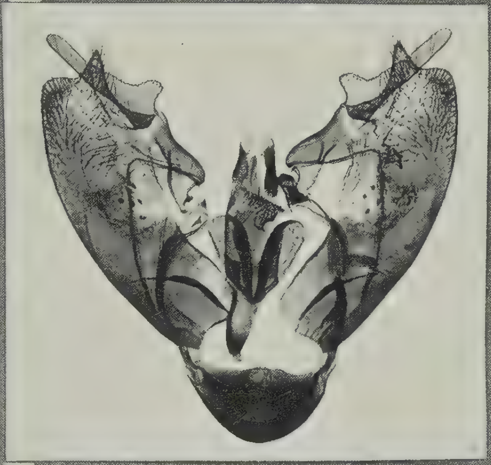
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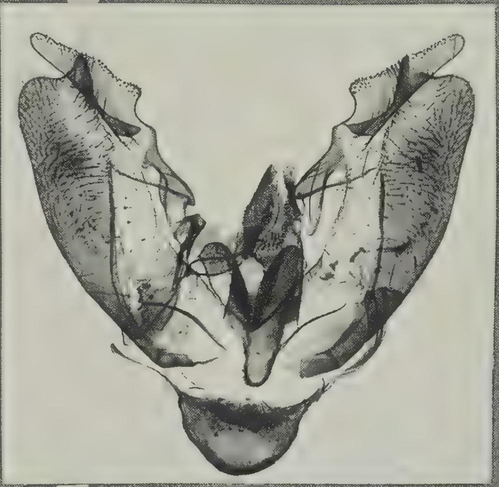
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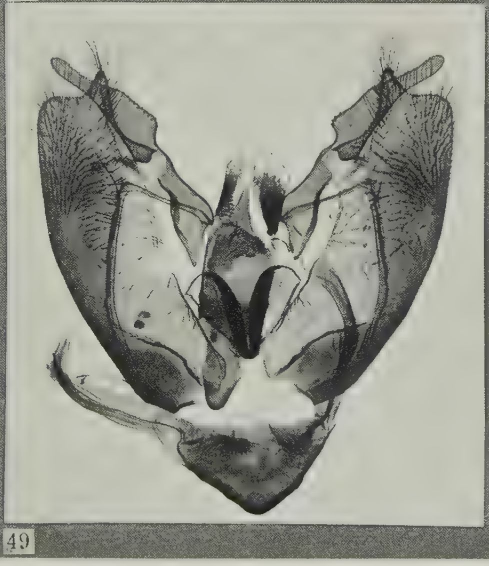
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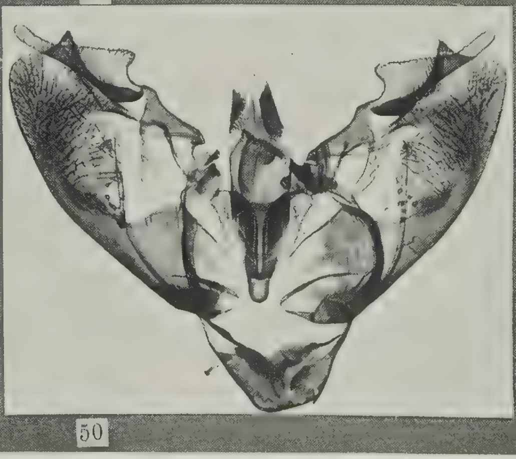
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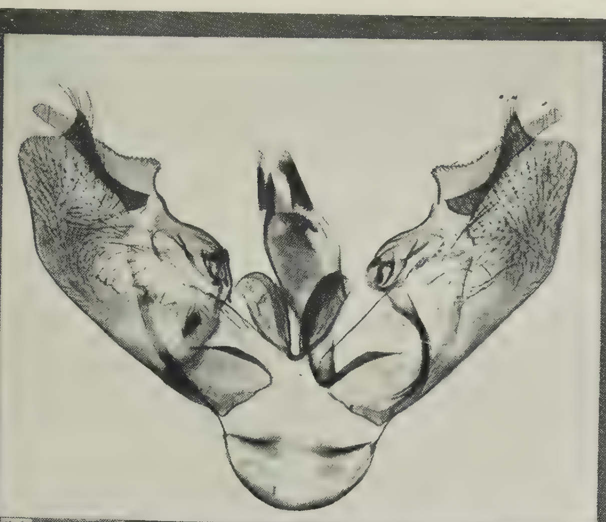

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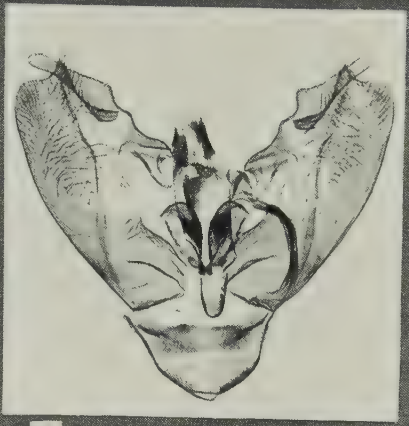

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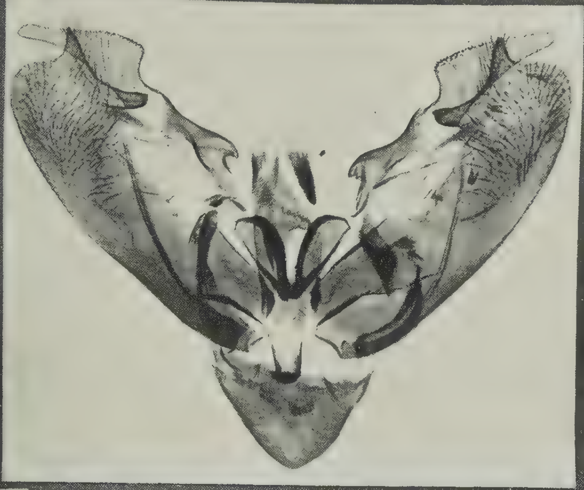

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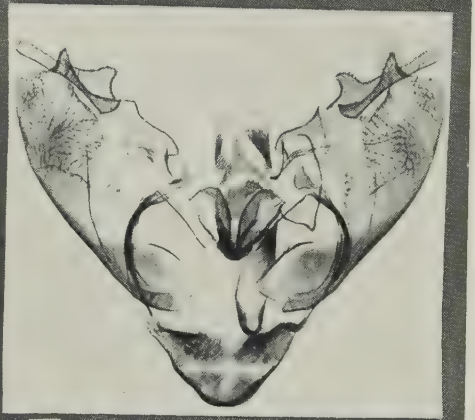

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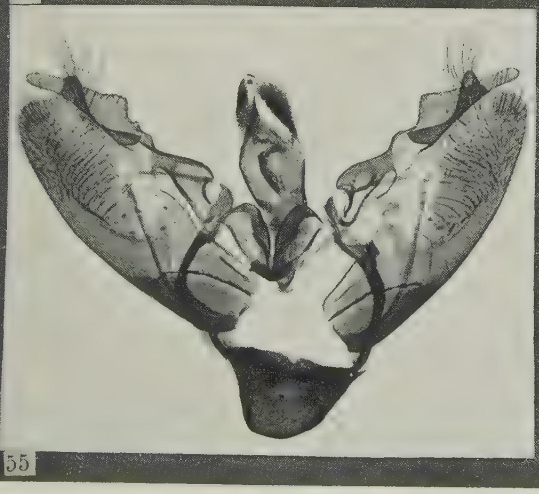

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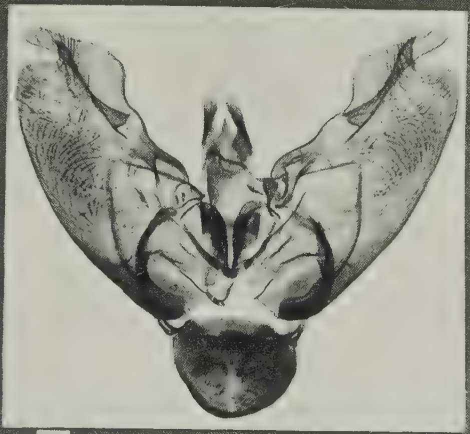

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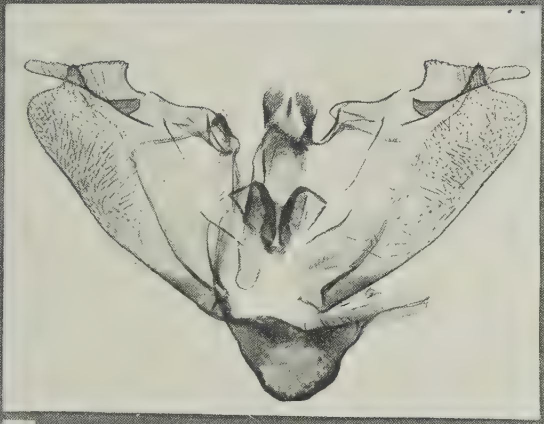
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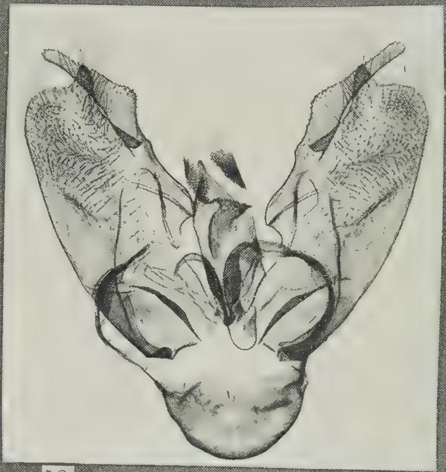
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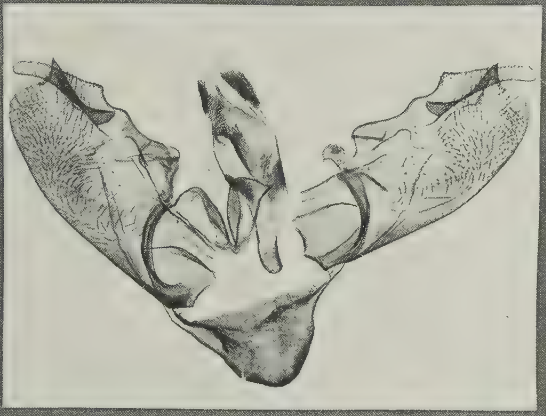
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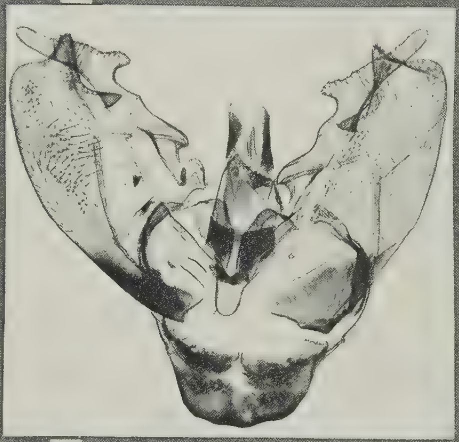
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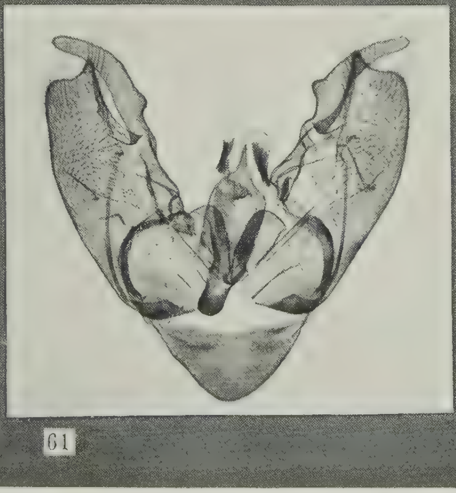
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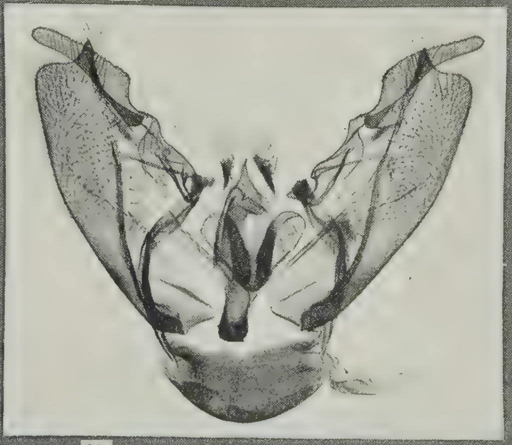
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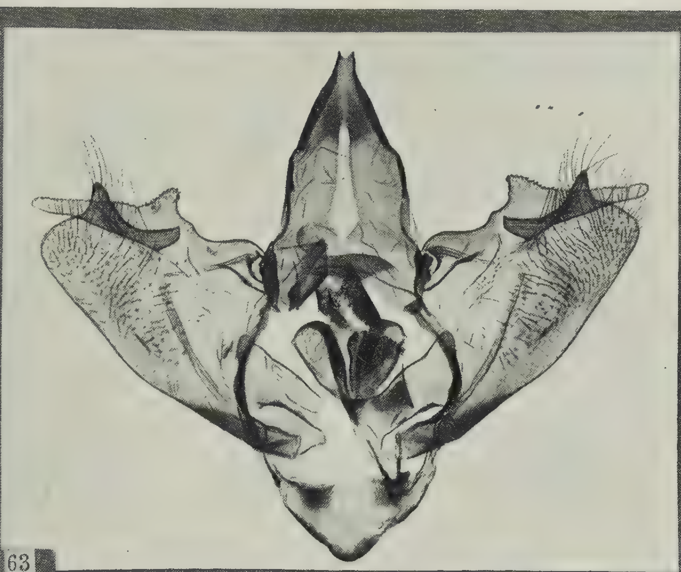
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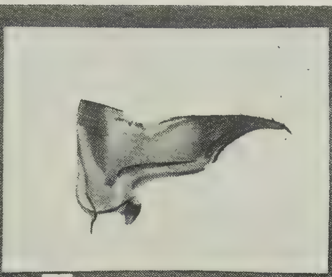
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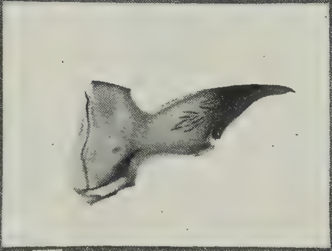
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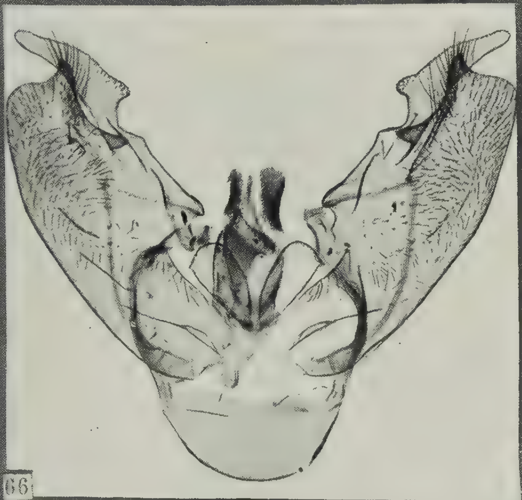
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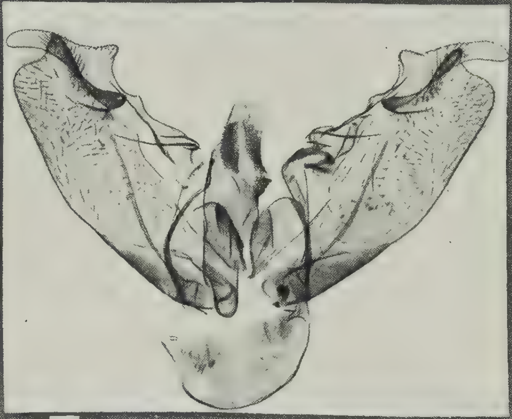
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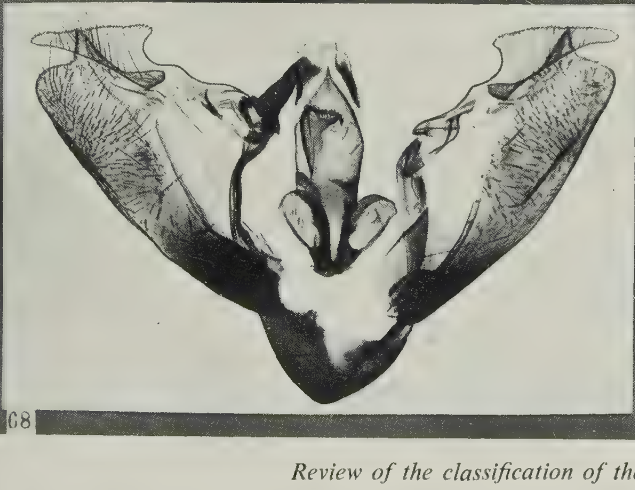
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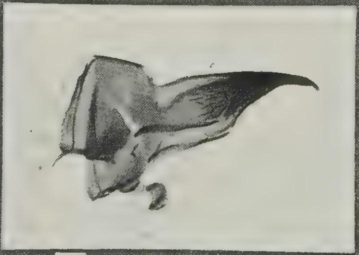
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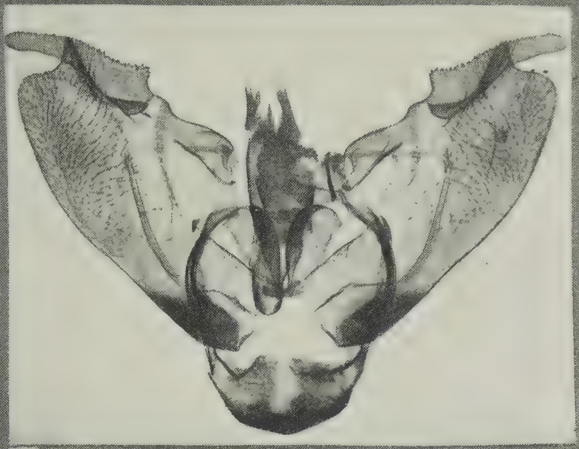
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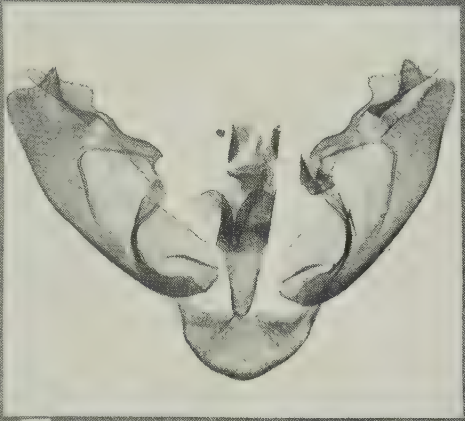
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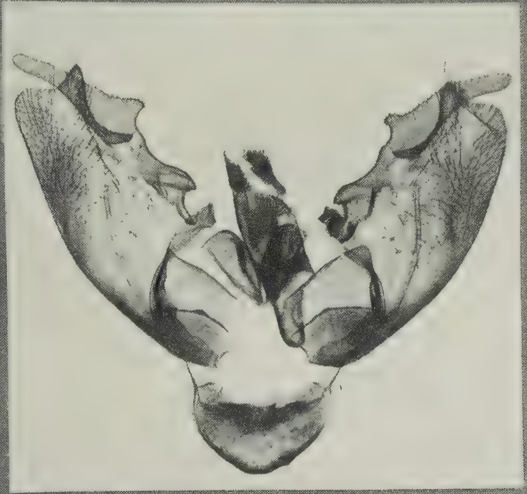
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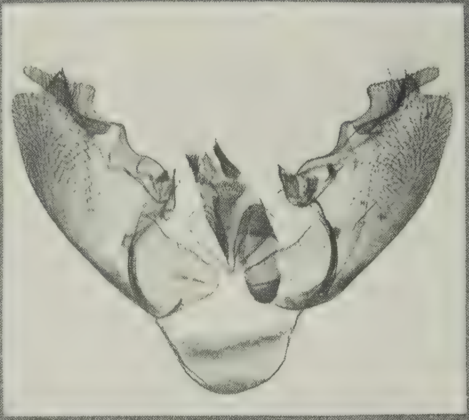
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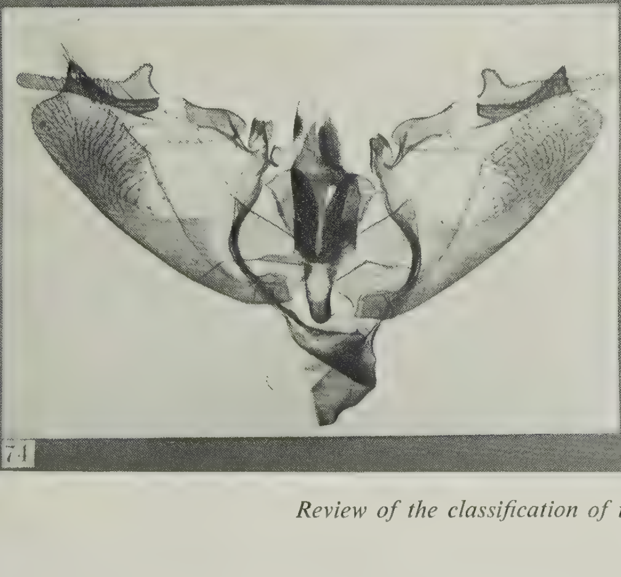
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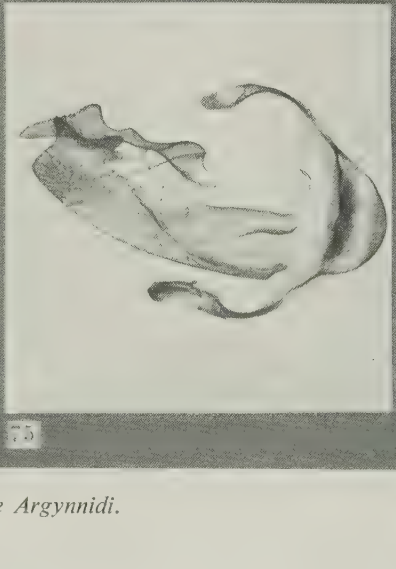
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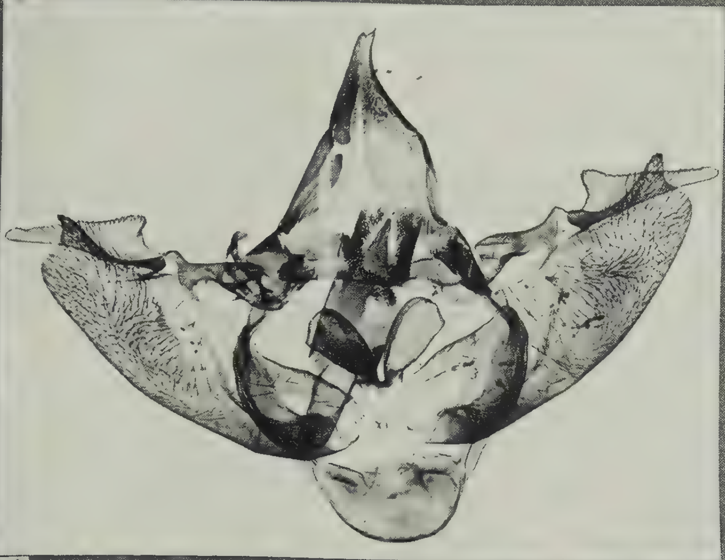

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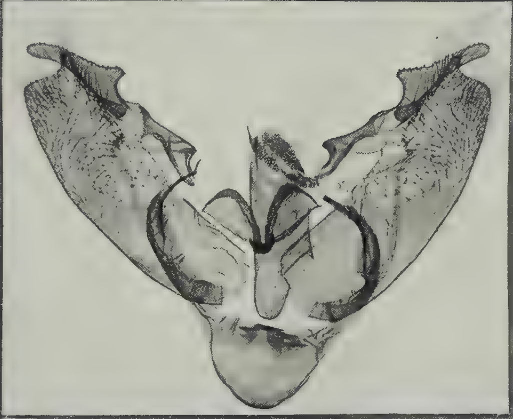

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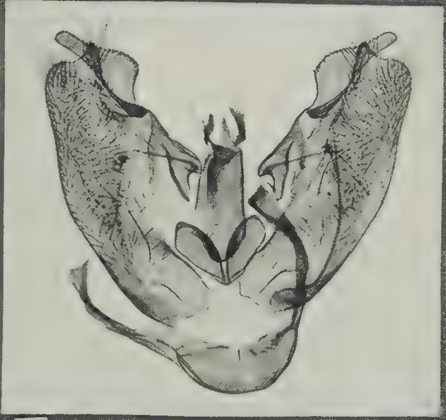

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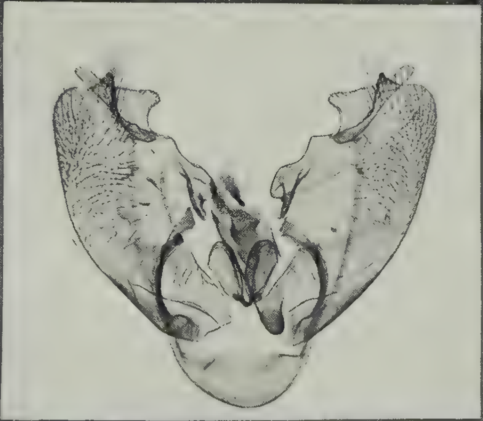

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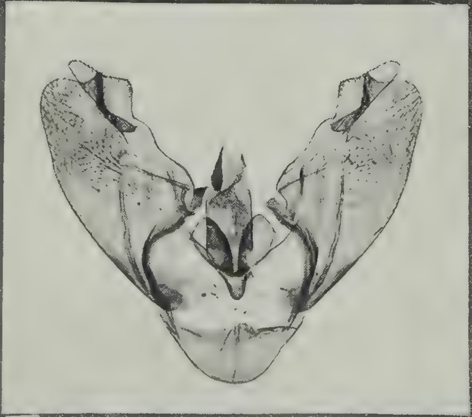

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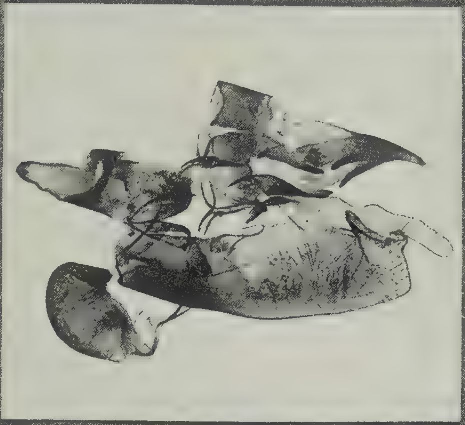

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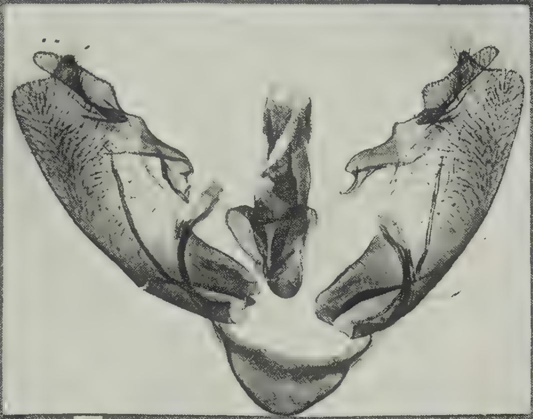

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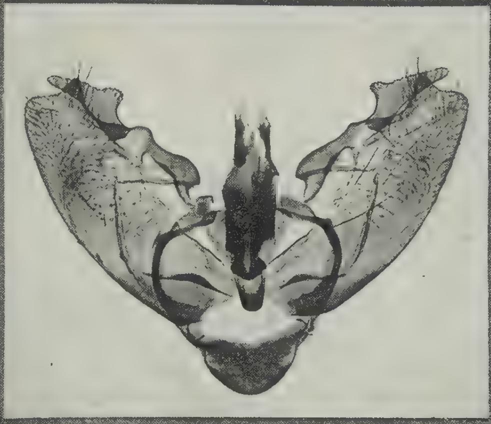

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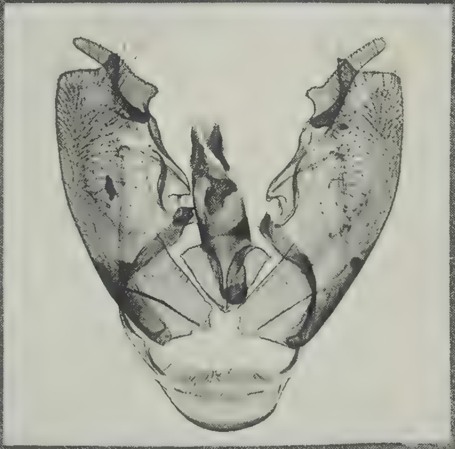

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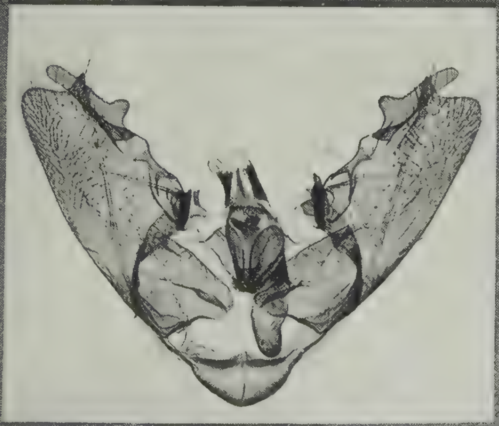

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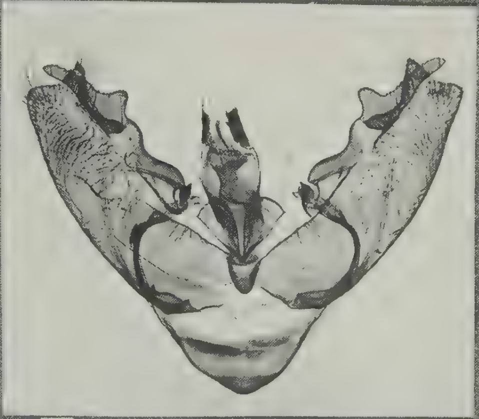

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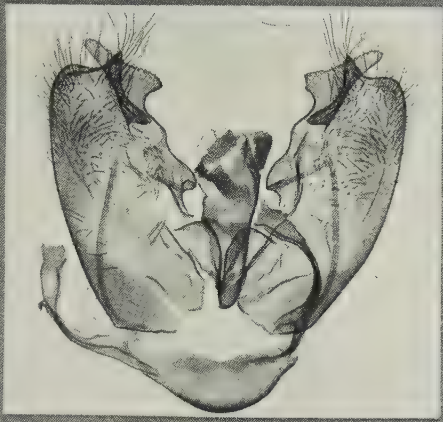

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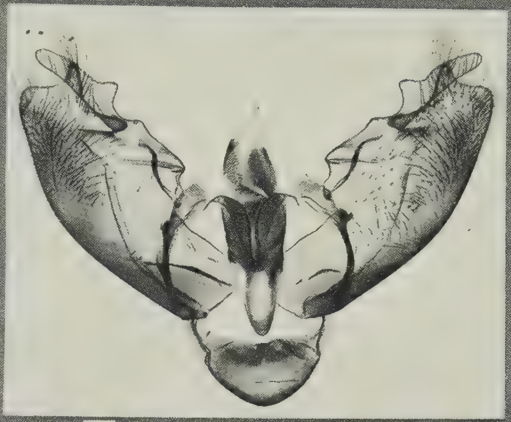

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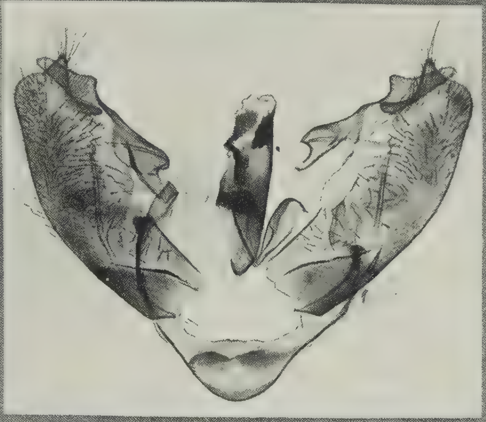

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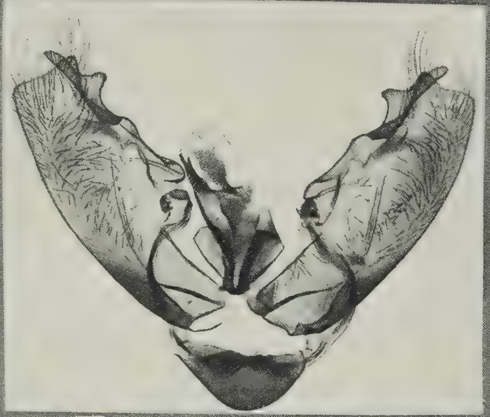

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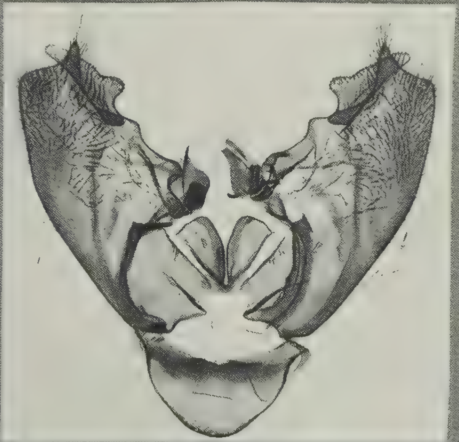

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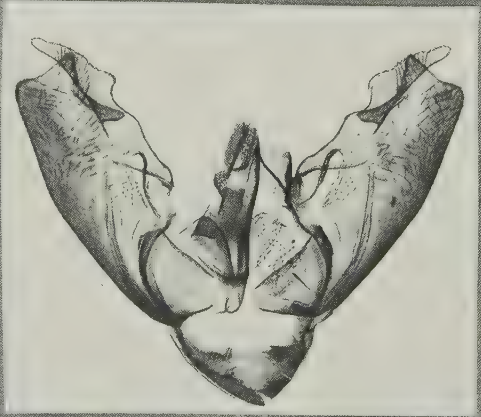

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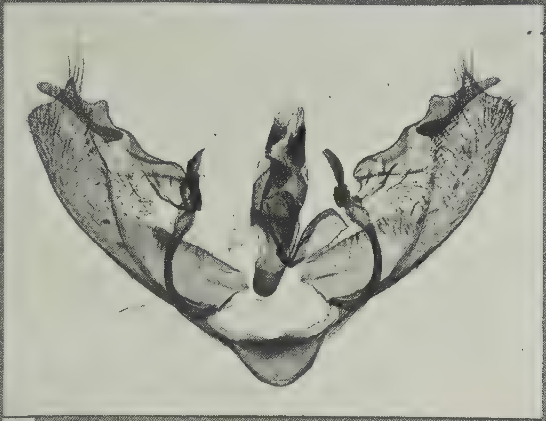
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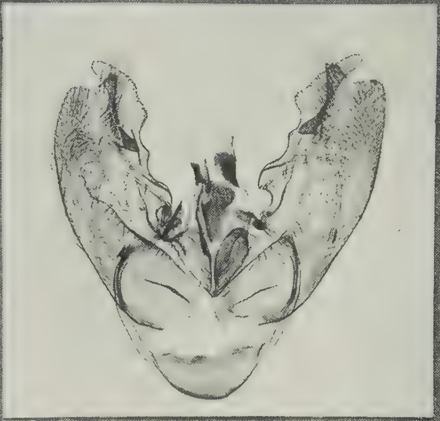
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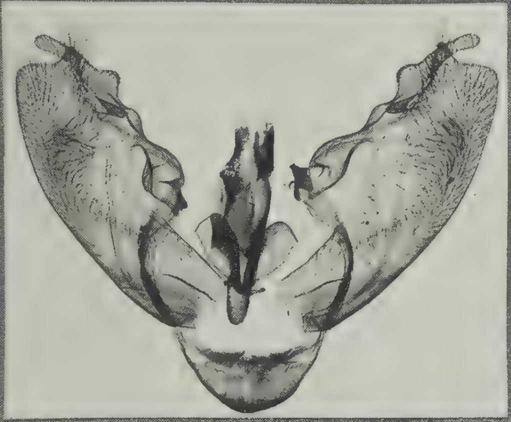
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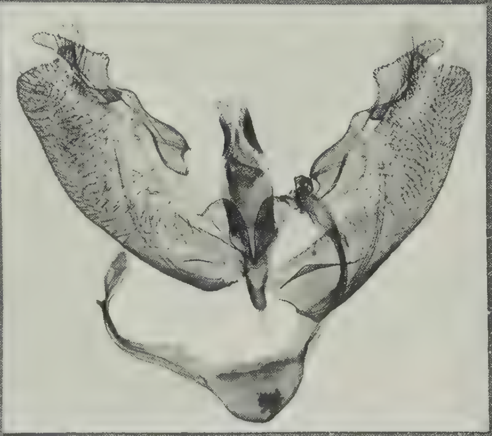
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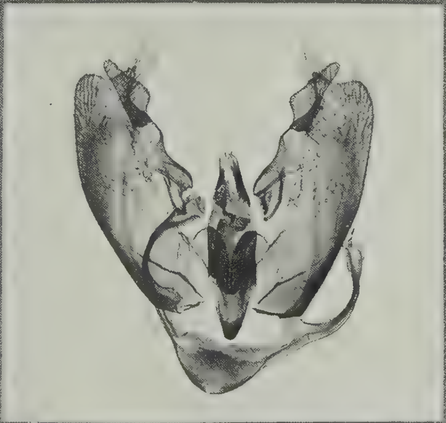
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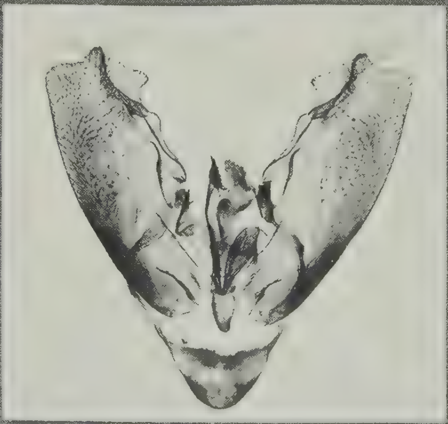
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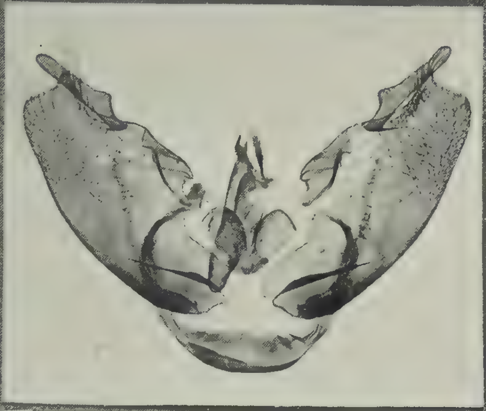
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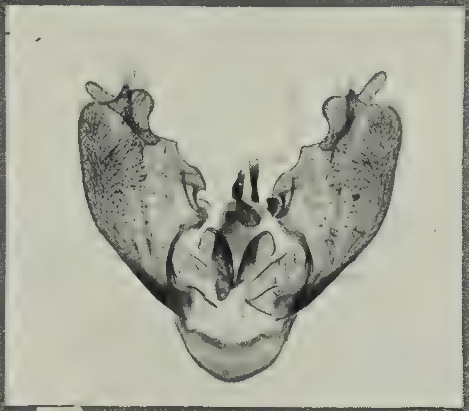
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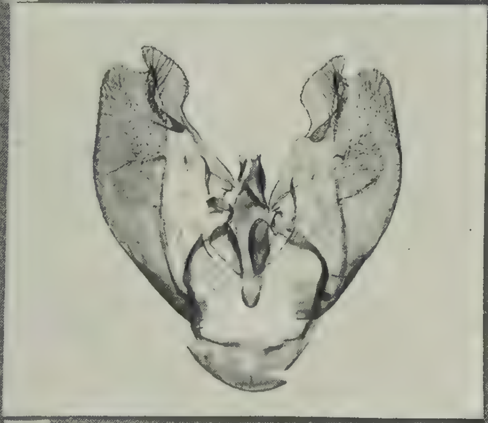
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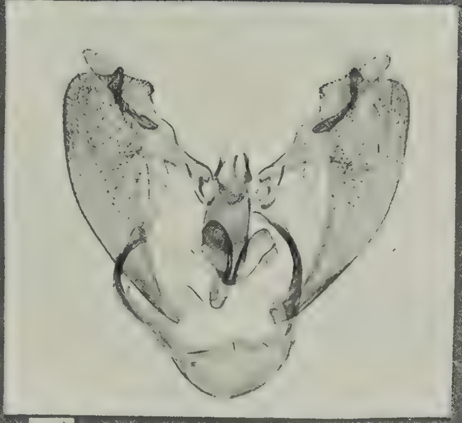
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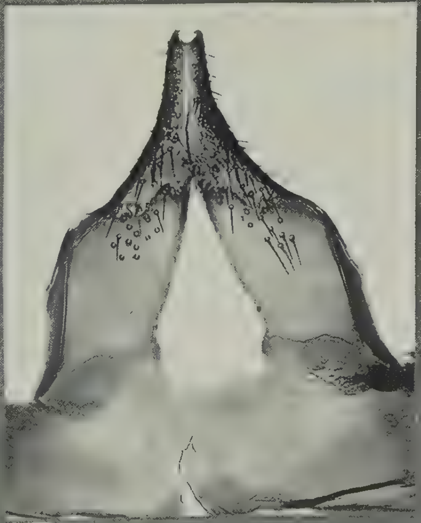
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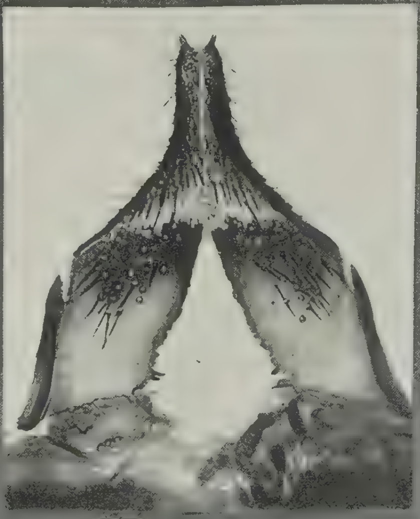
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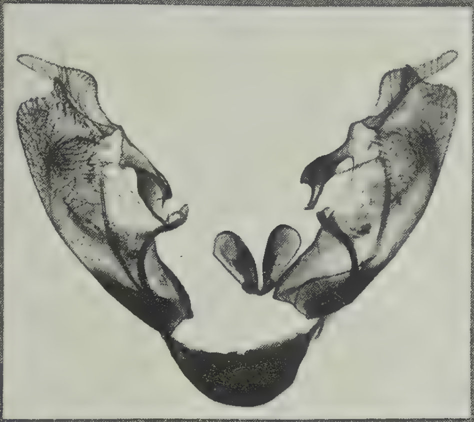

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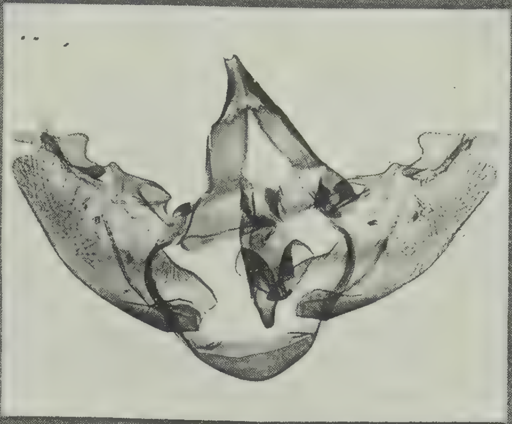

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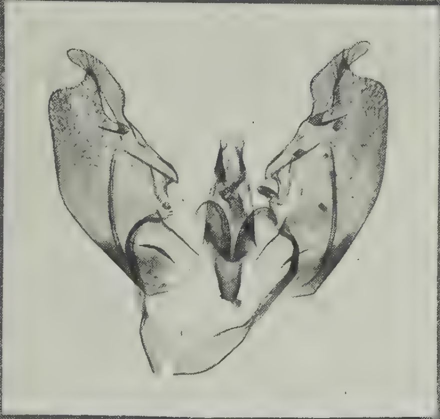

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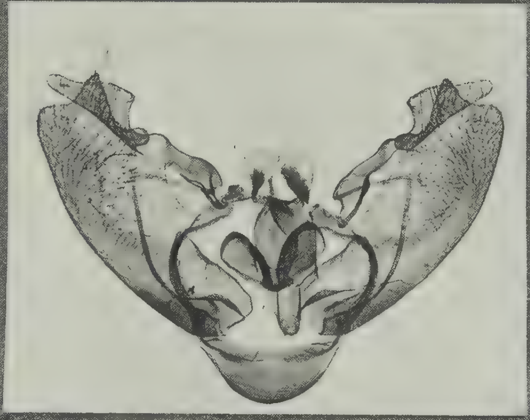

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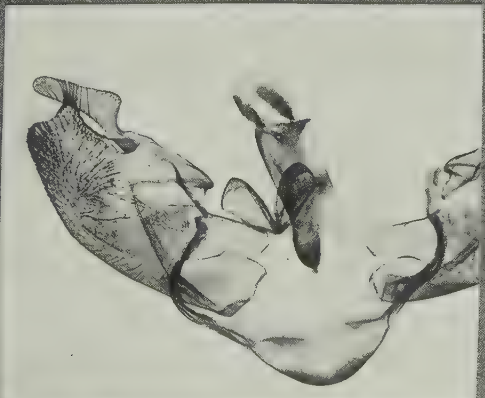

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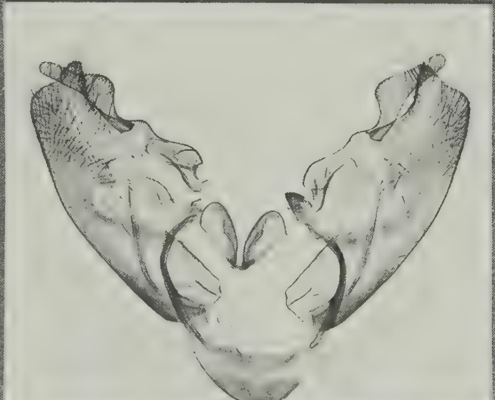
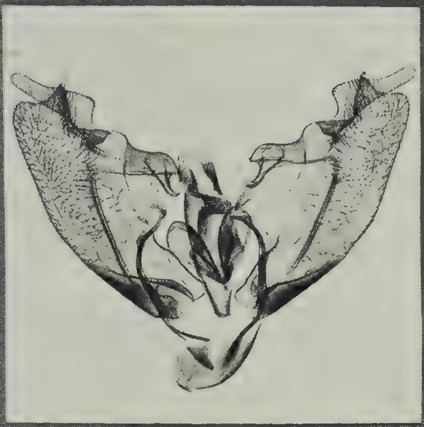


110

Review of the classification of the Argynnidi.



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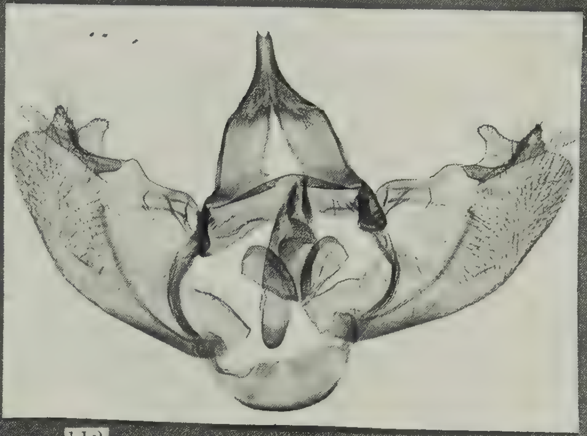

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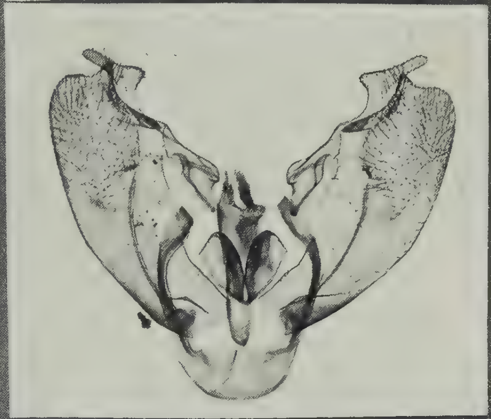

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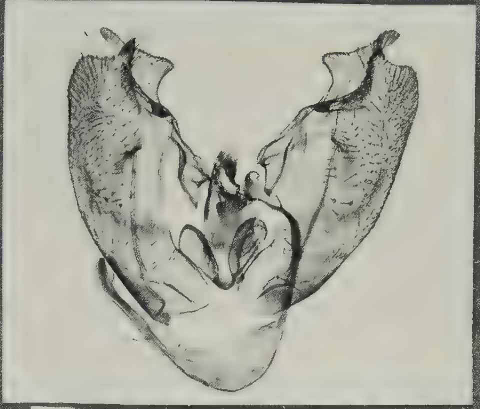

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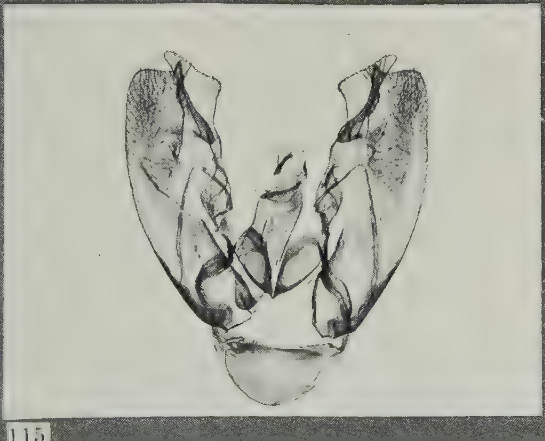

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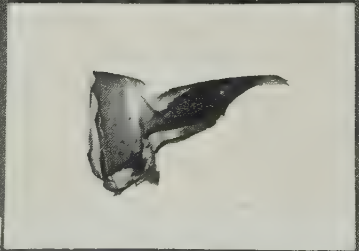

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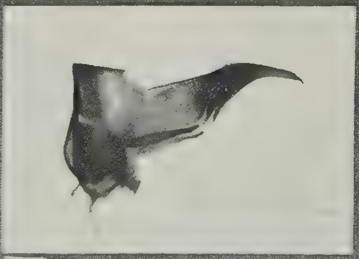

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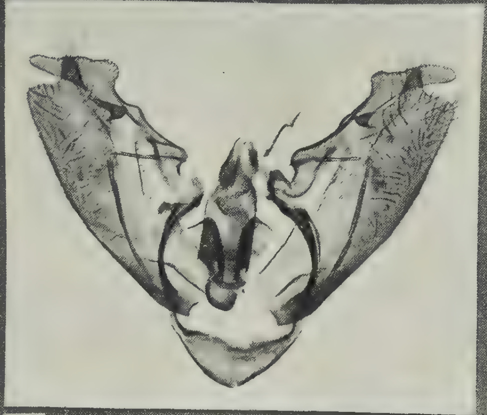
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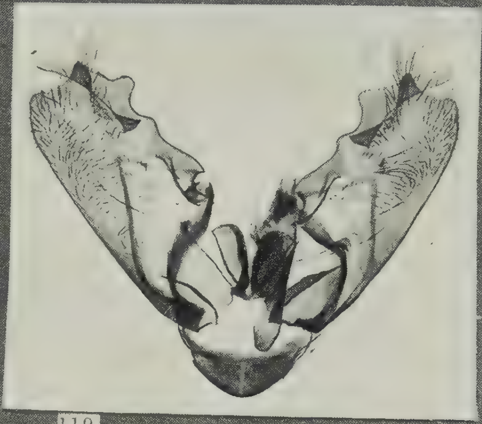
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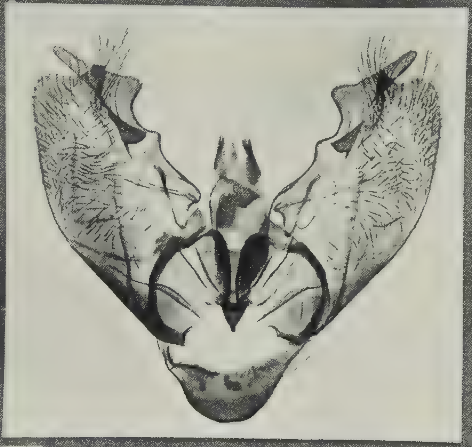
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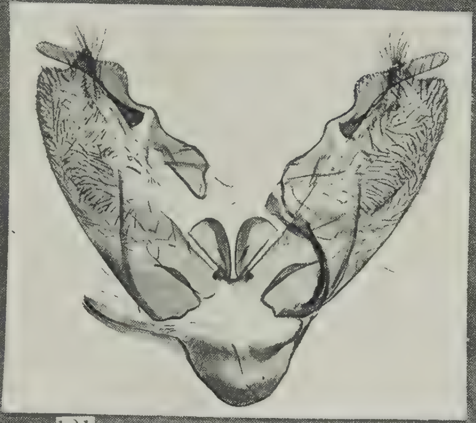
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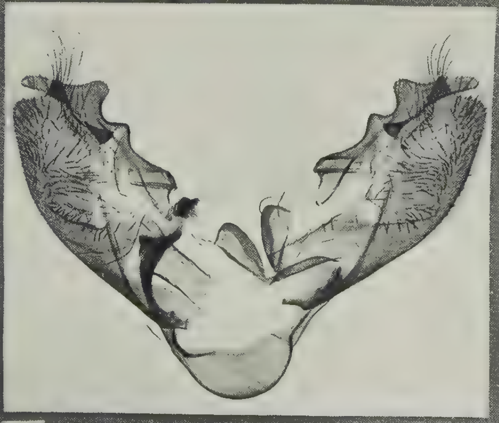
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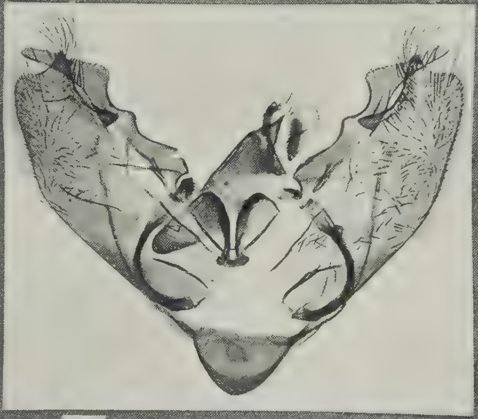
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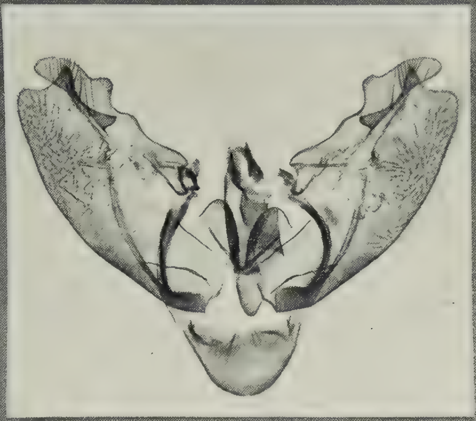

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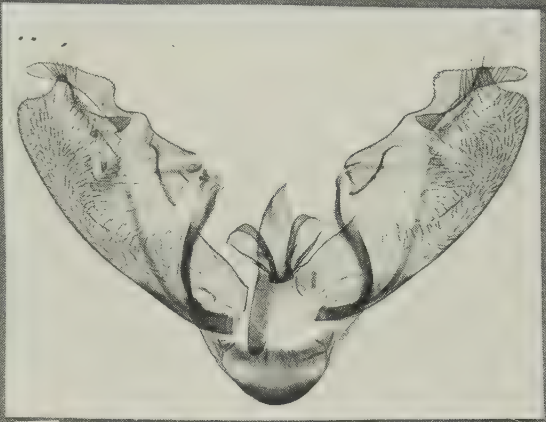

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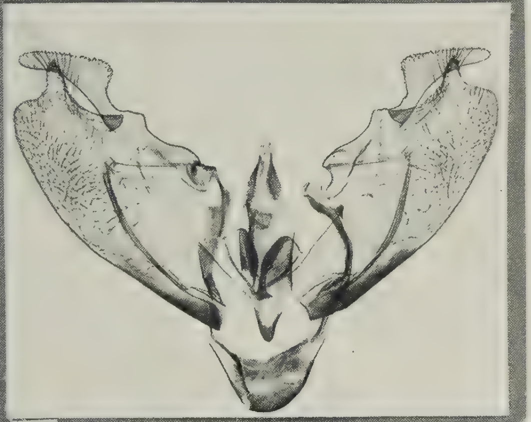

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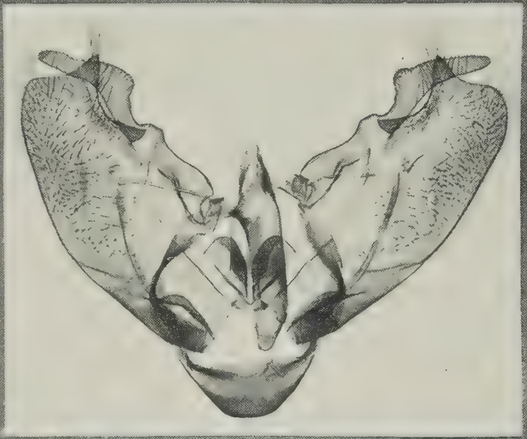

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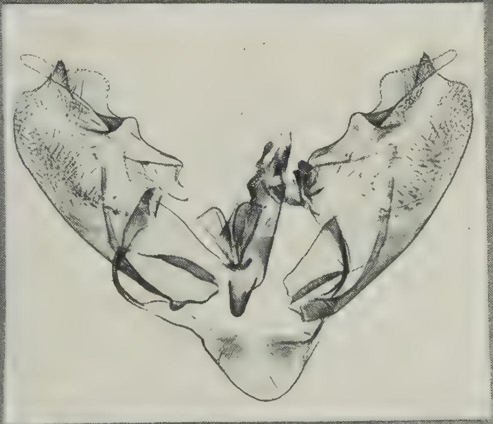

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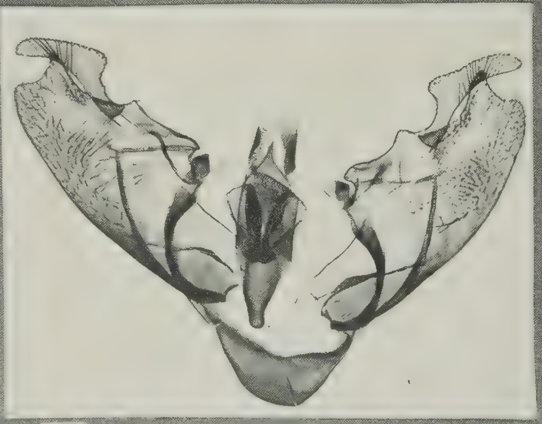

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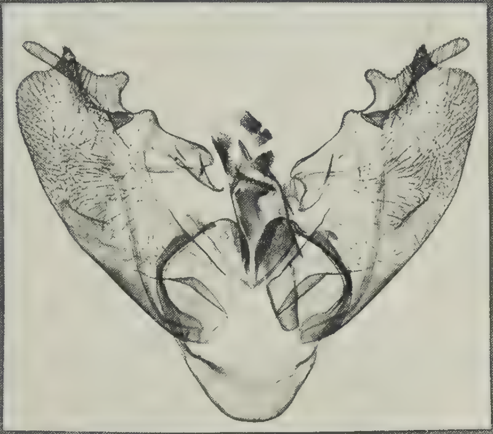
Review of the classification of the Argynnidi.



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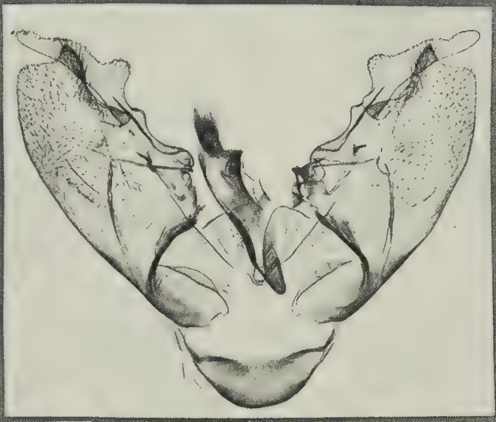

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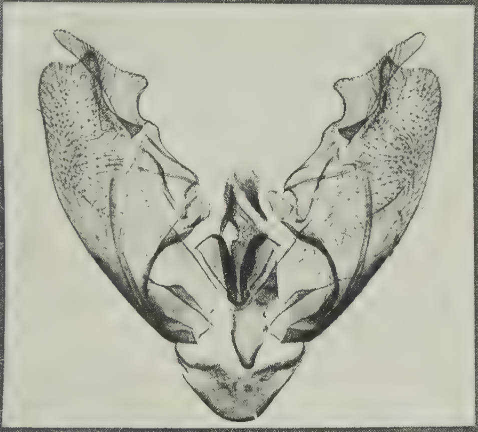

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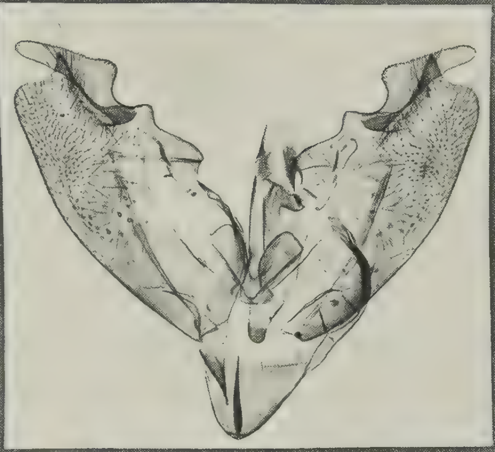

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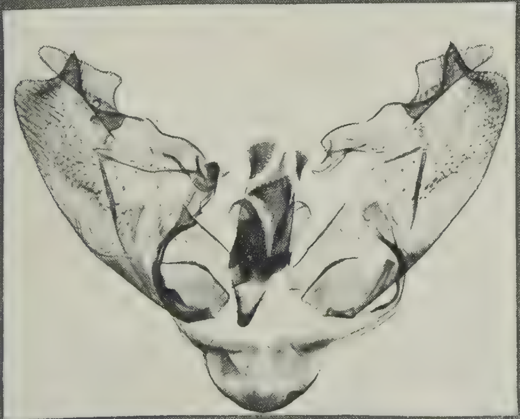

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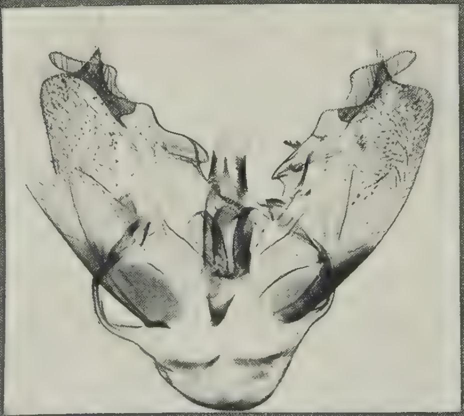

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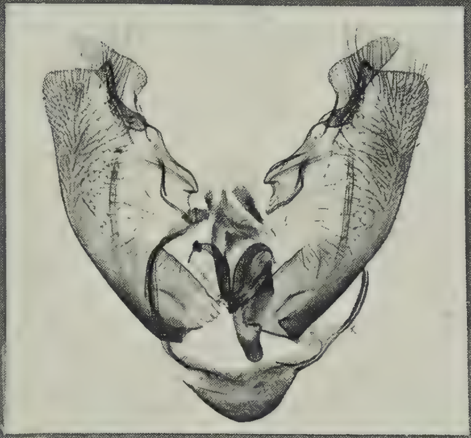
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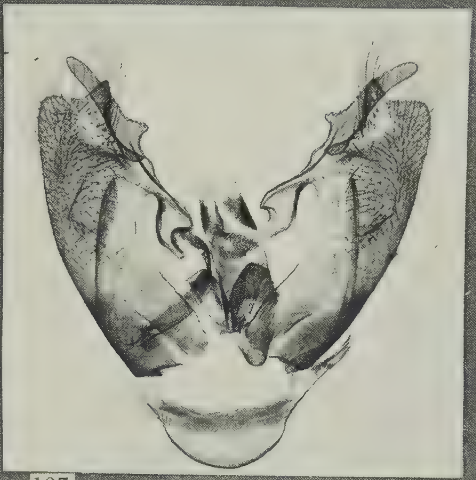
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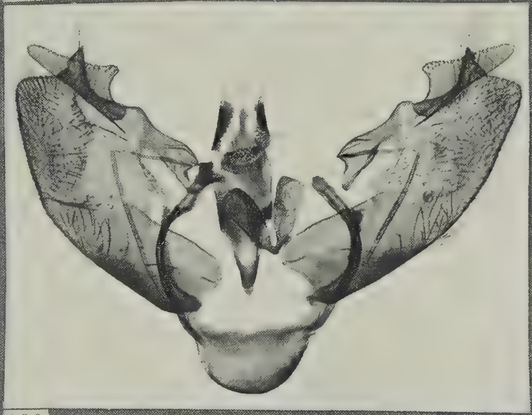
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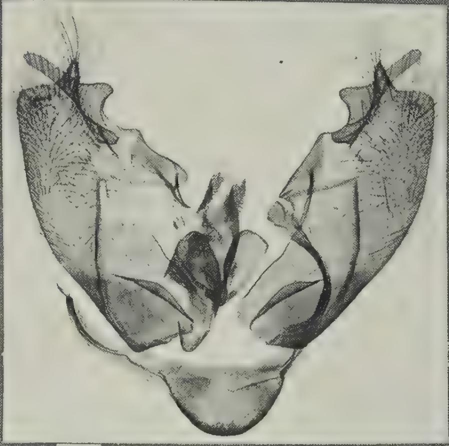
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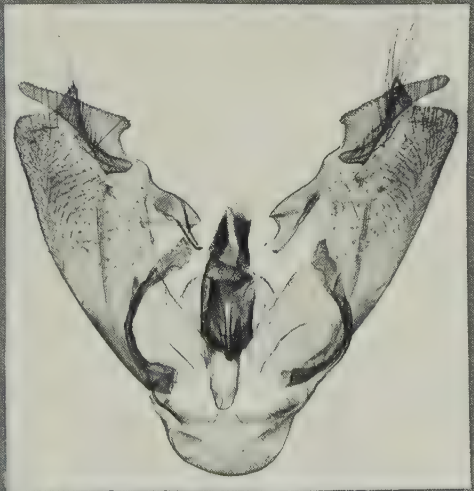
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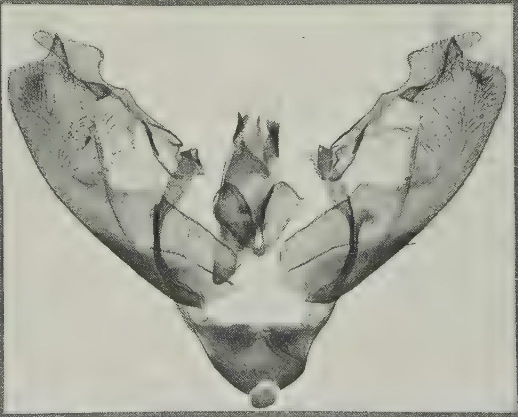
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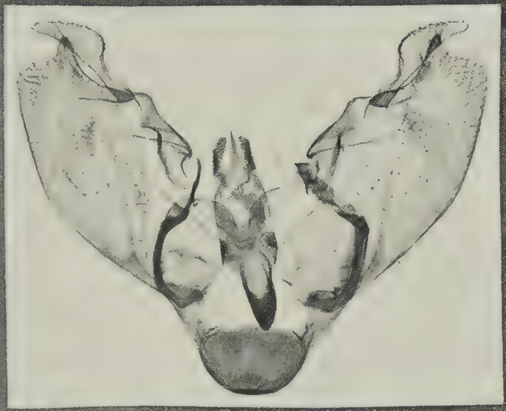
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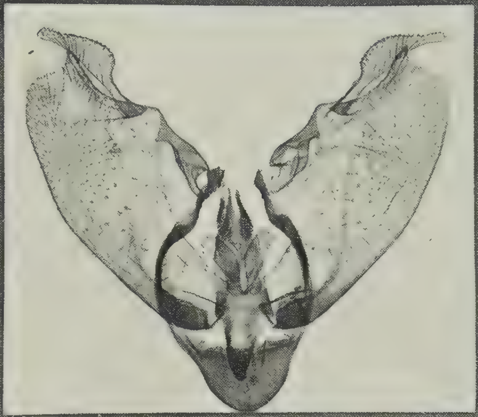
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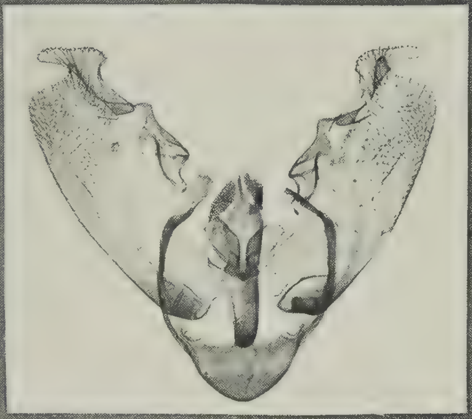
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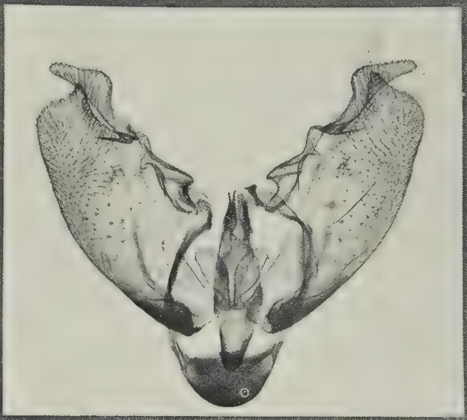
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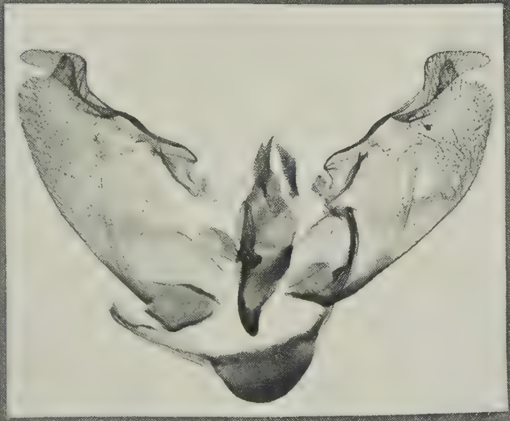
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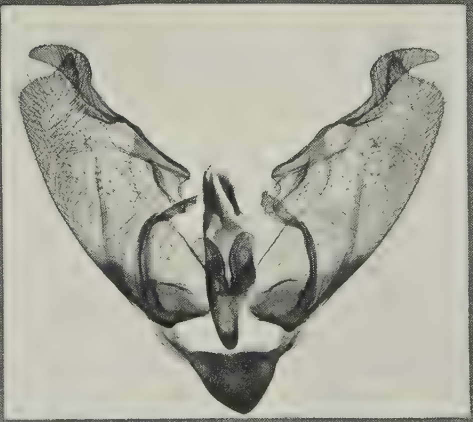
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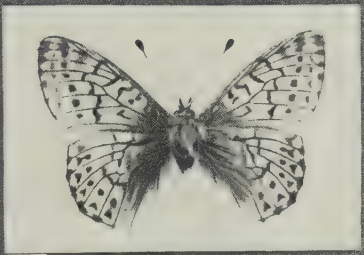
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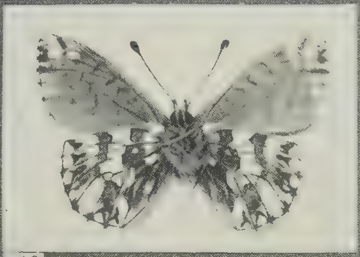
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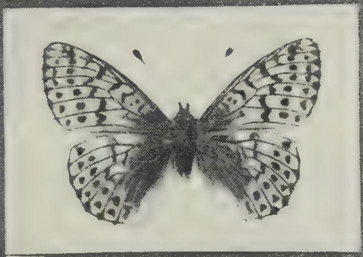
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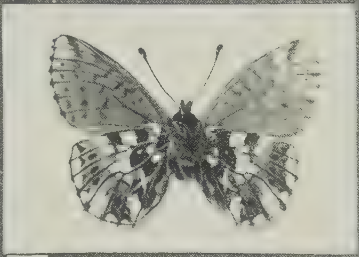
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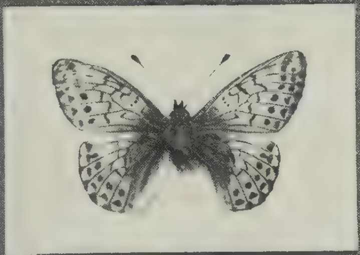
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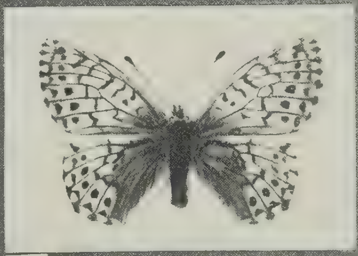
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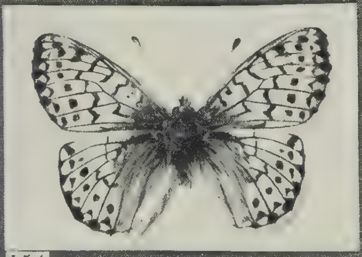
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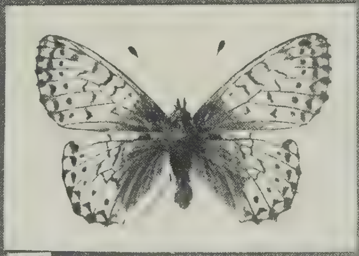
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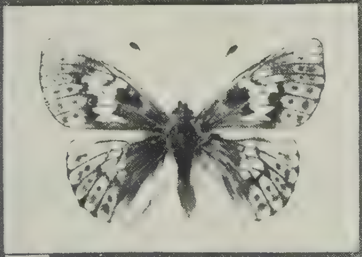
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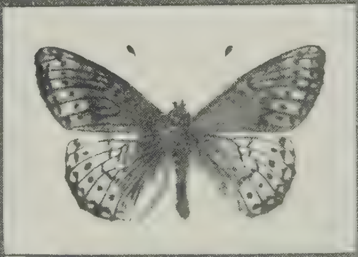
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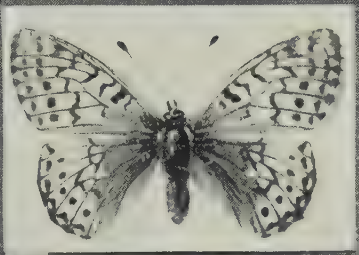
Review of the classification of the Argynnidi.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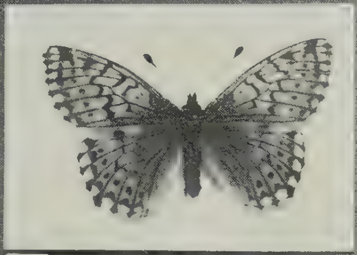
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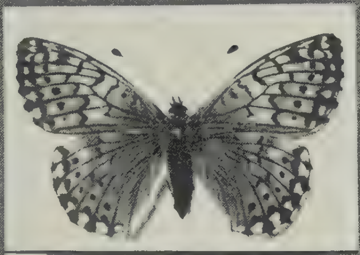
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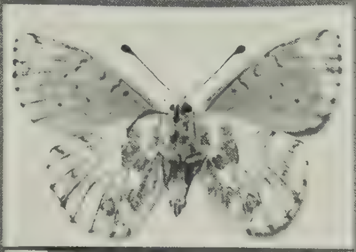
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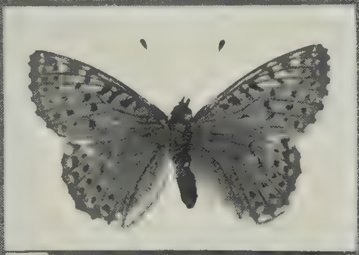
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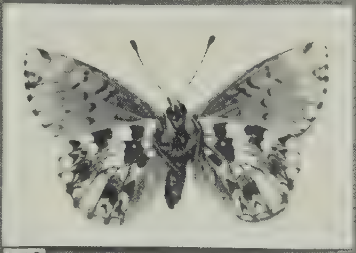
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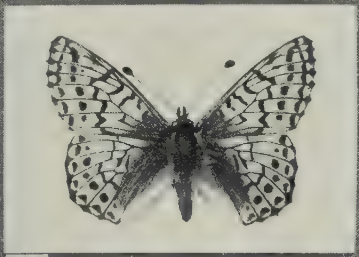
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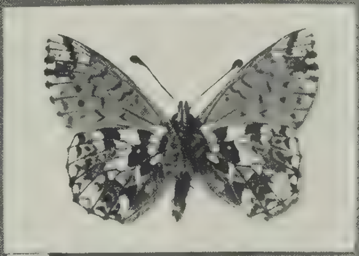
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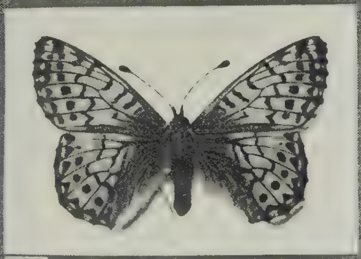
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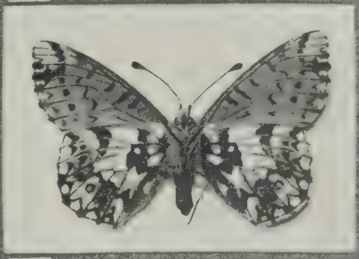
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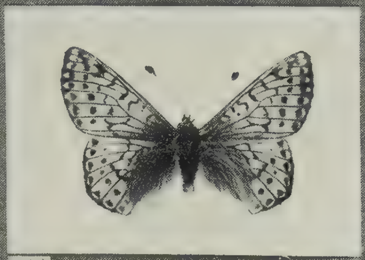

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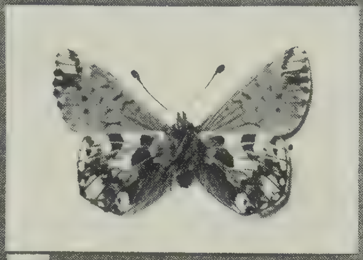

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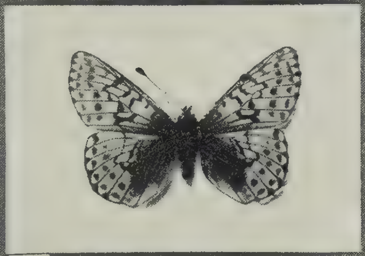

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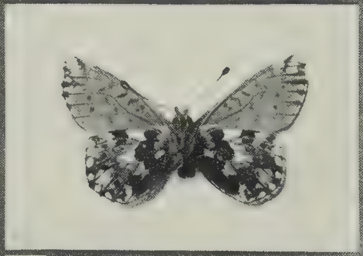

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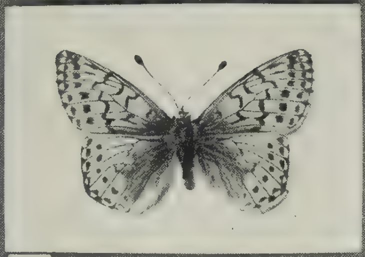

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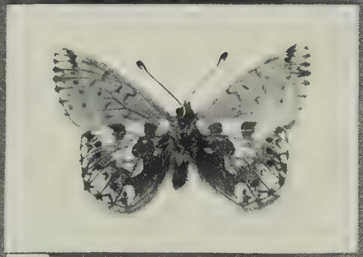

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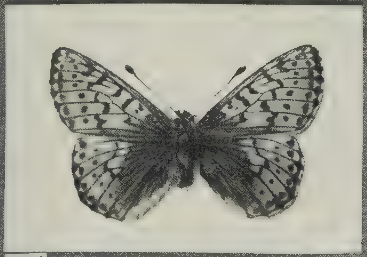

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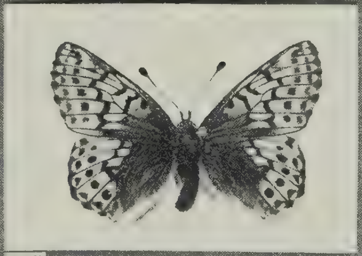

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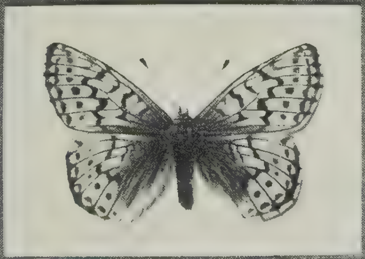

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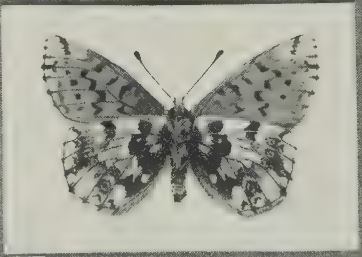

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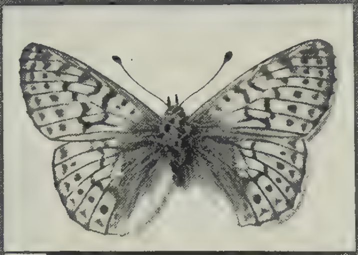
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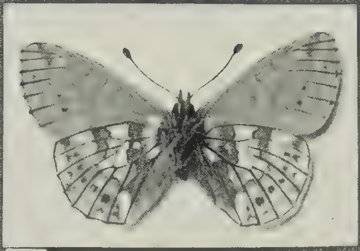
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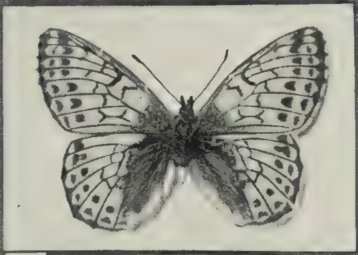
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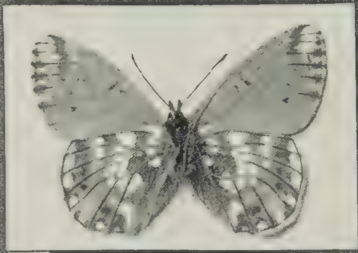
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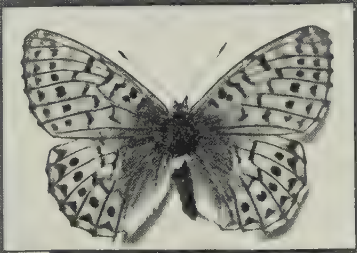
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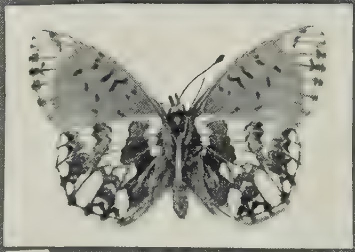
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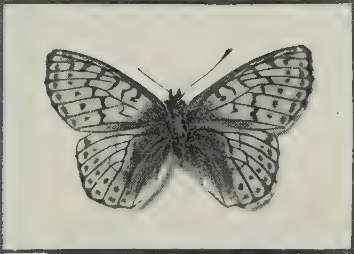
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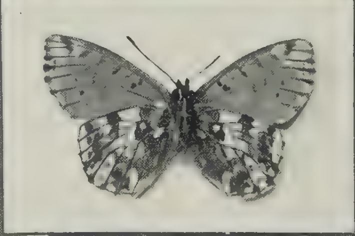
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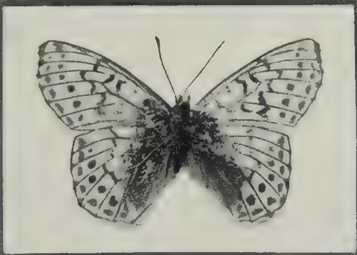
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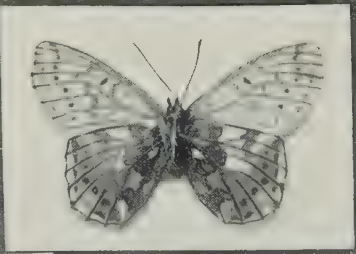
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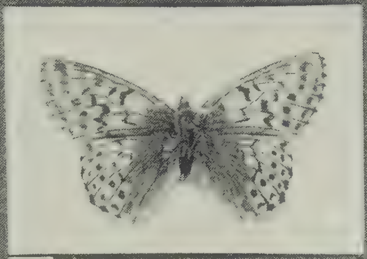
Review of the classification of the Argynnidi.



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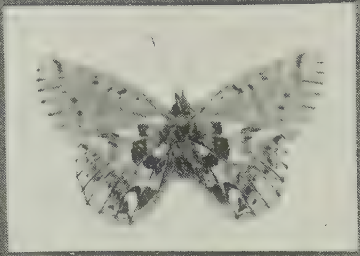

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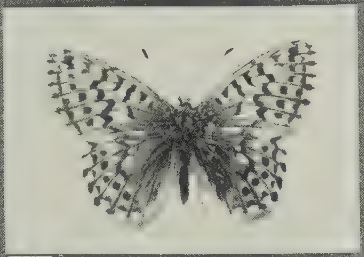

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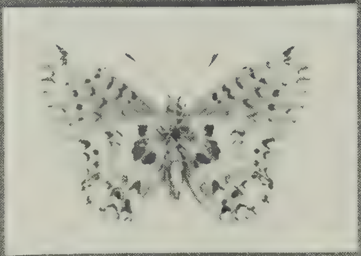

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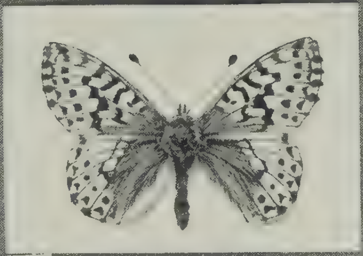

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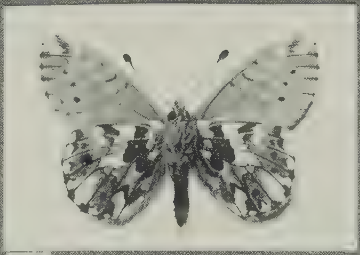

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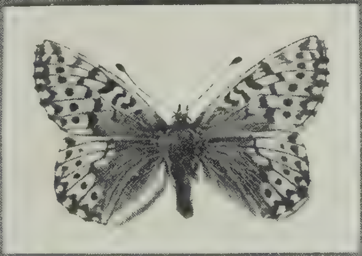

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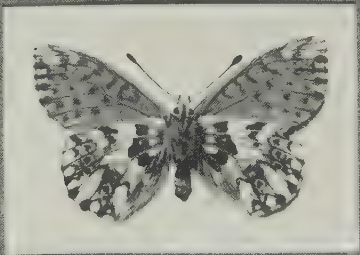

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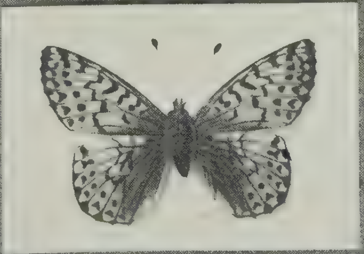

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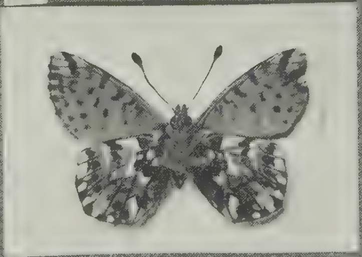

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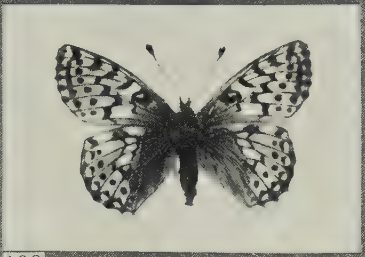
Review of the classification of the Argynnidi.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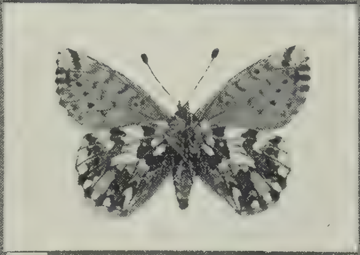
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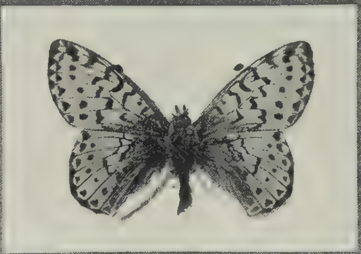
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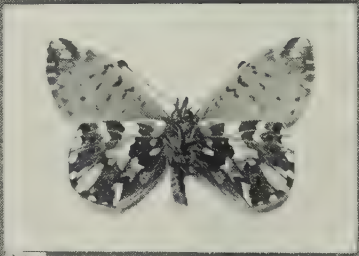
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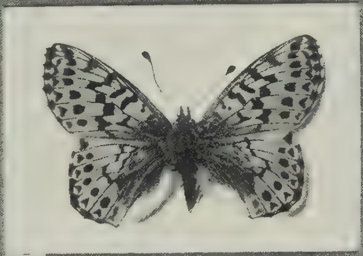
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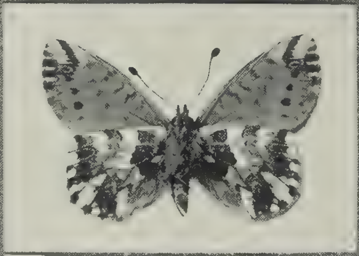
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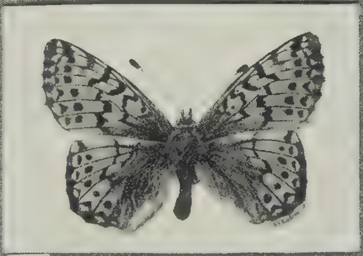
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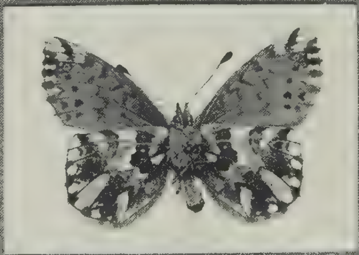
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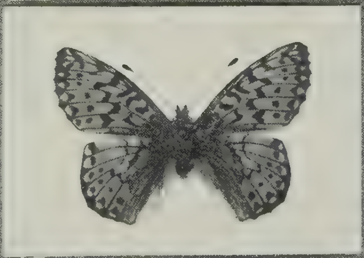
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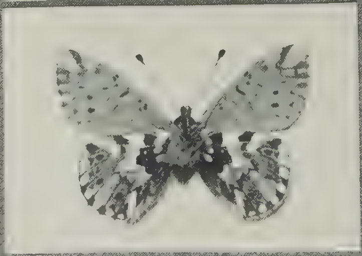
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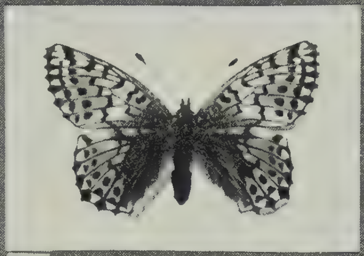
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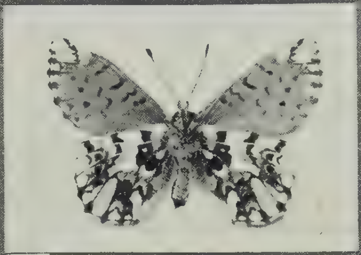
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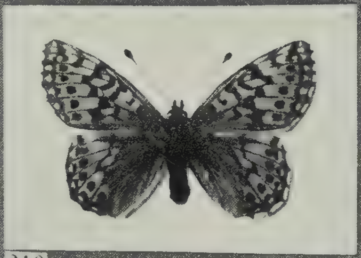
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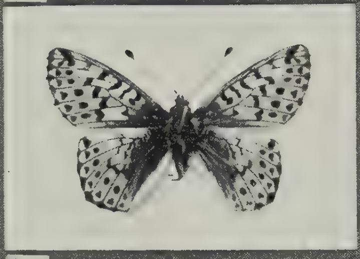
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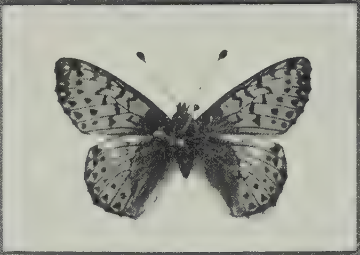
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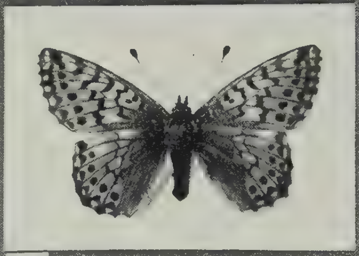
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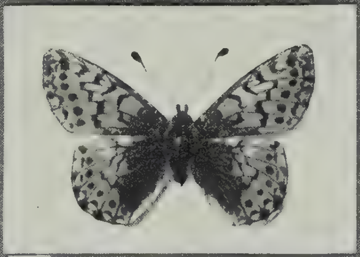
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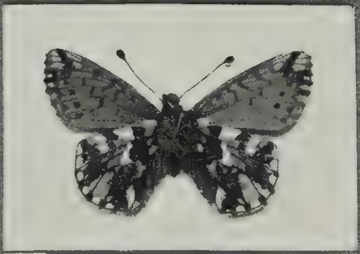
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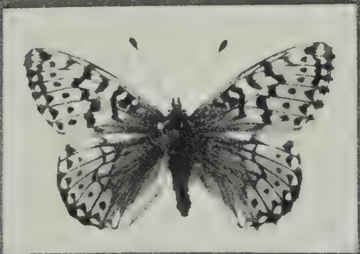
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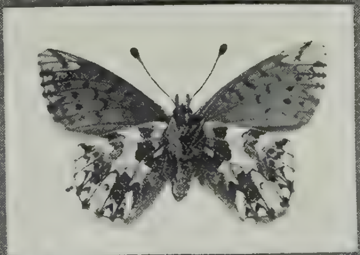
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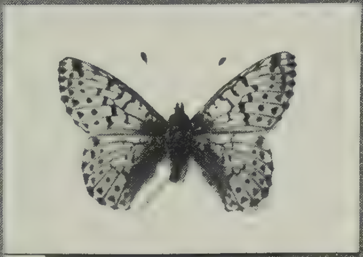
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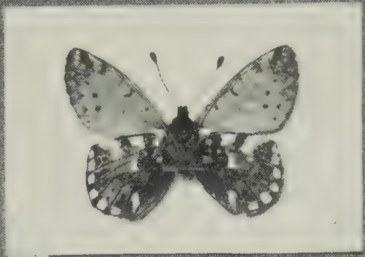
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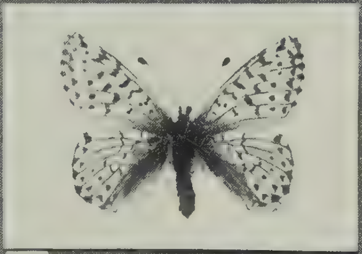
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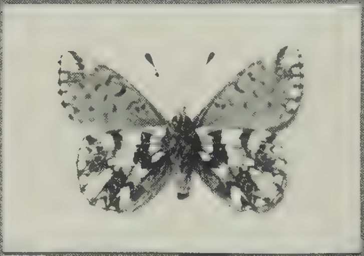
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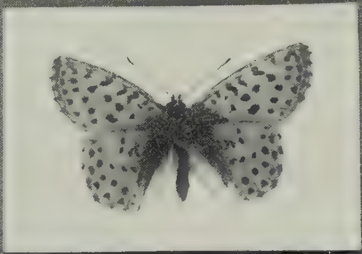
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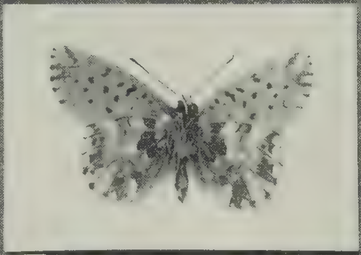
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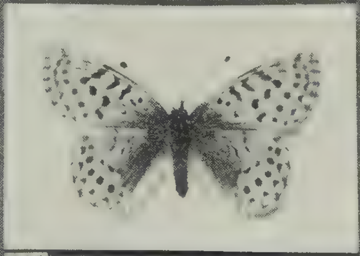
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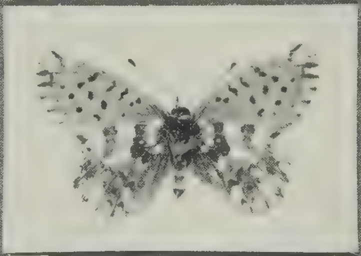
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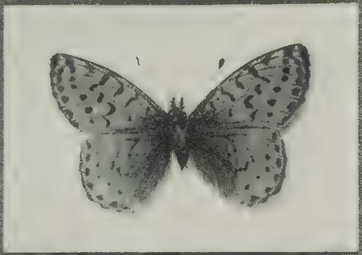
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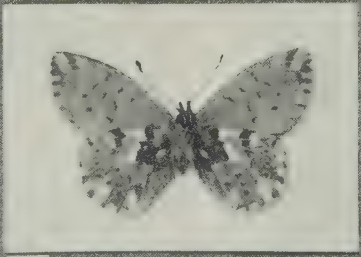
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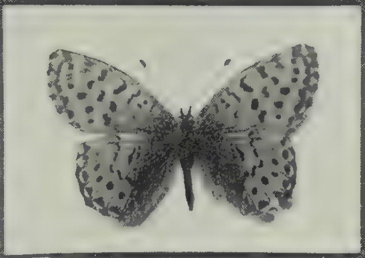
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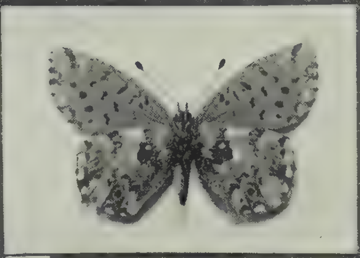
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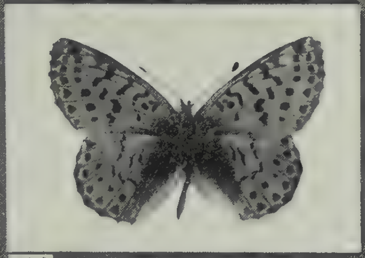
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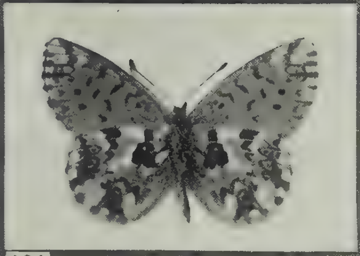
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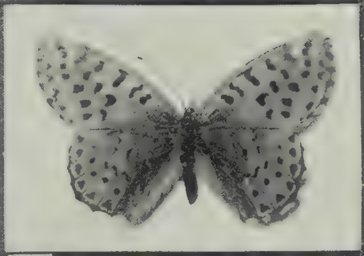
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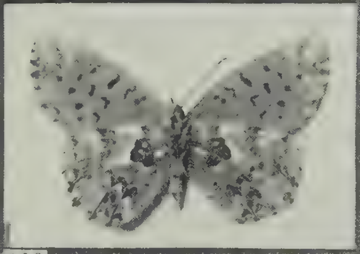
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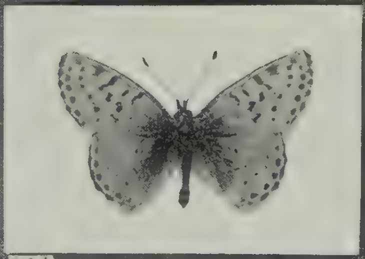
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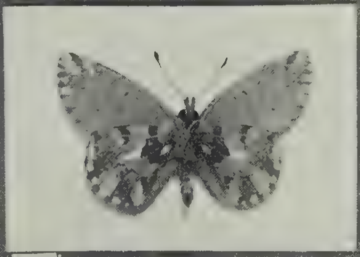
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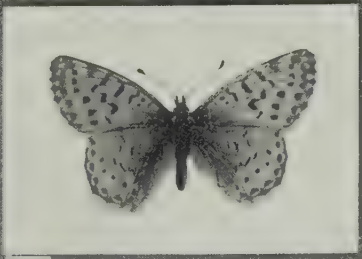
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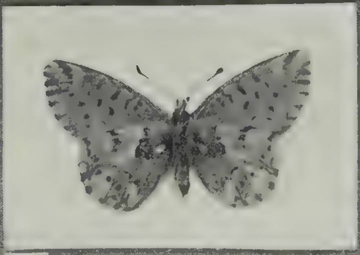
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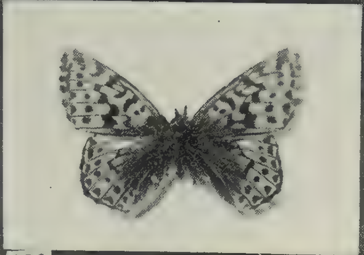
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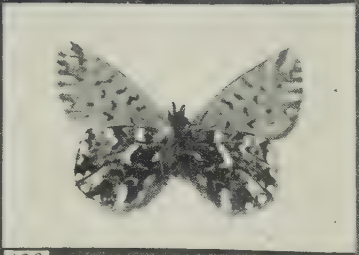
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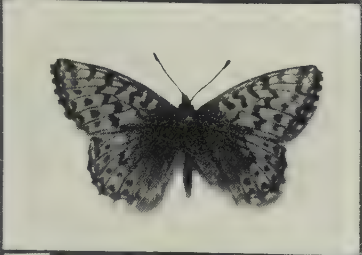
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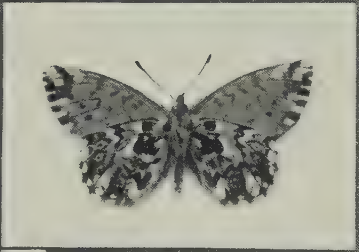
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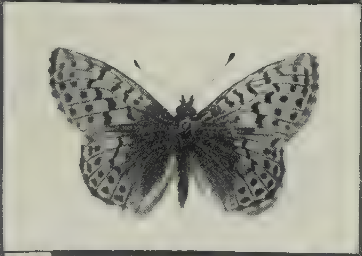
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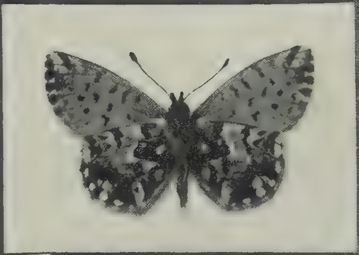
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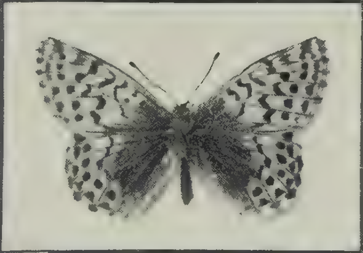
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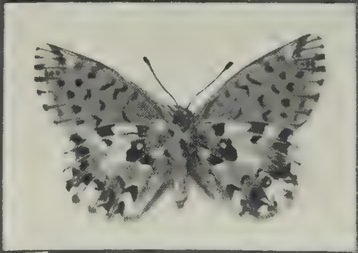
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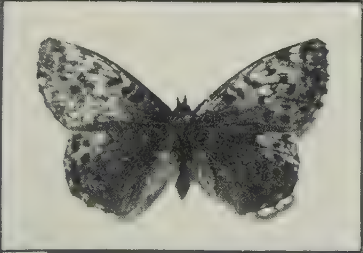
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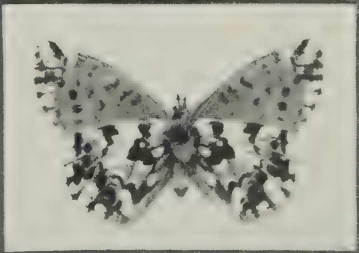
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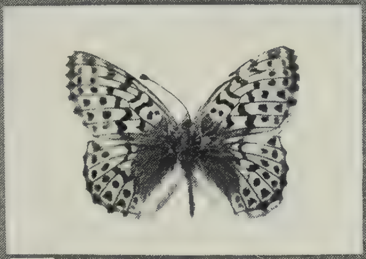
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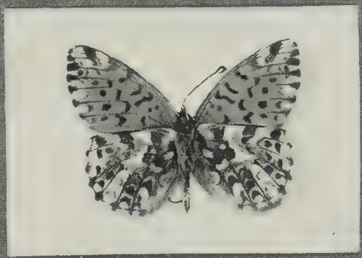
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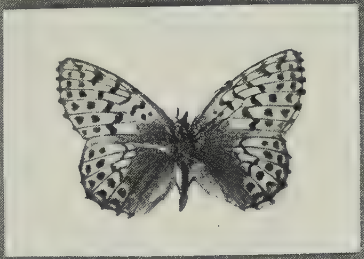
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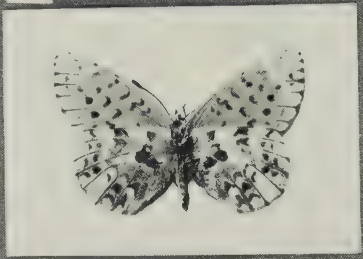
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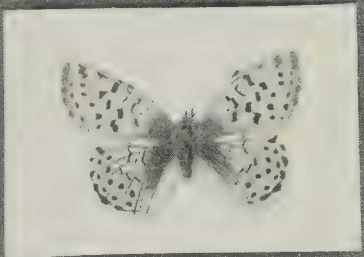
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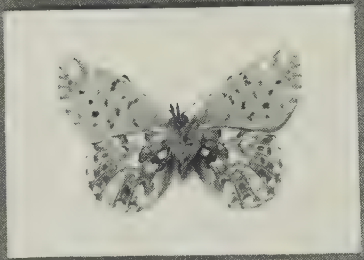
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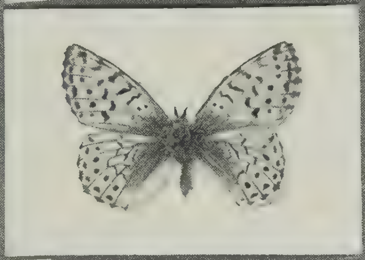
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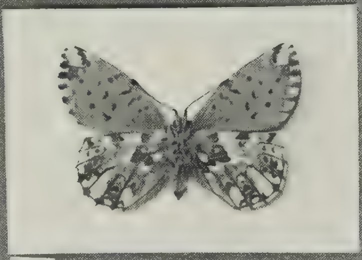
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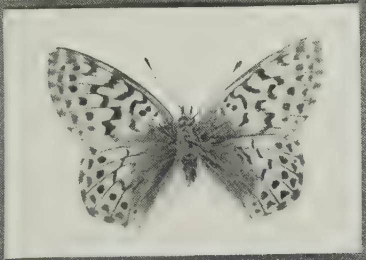
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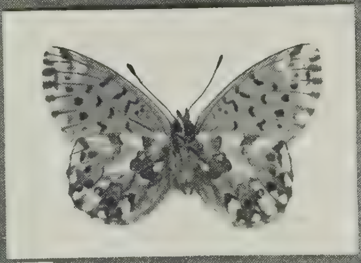
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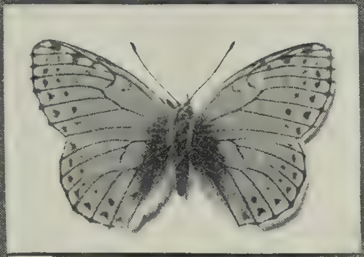
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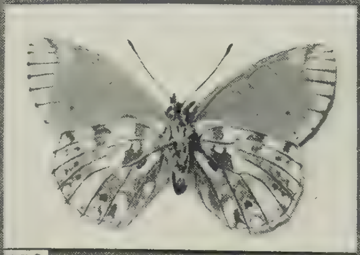
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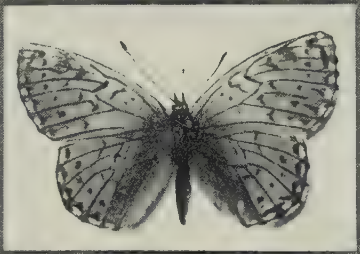
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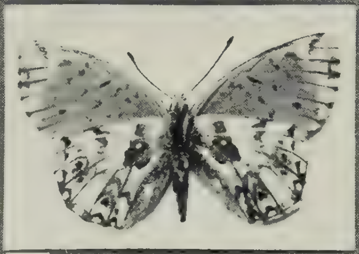
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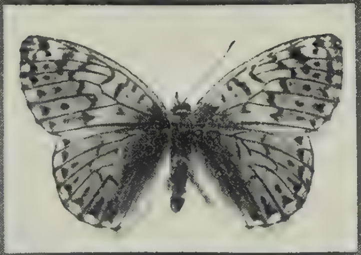
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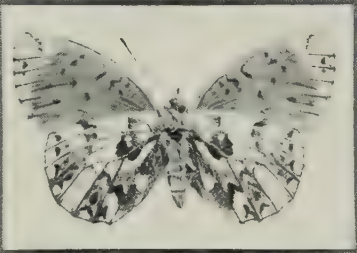
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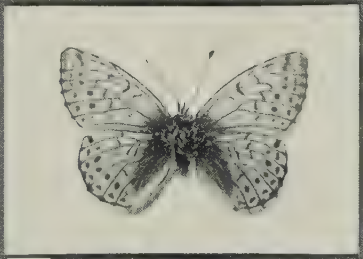
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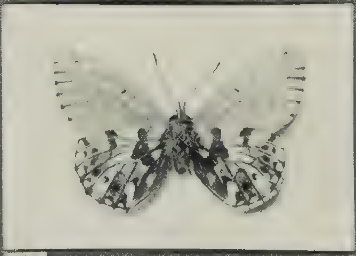
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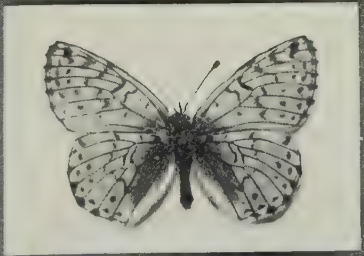
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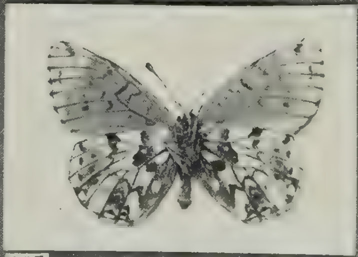
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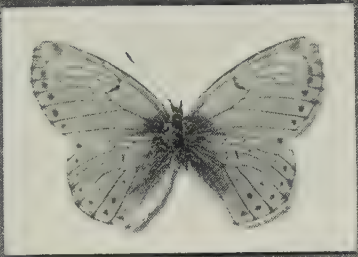
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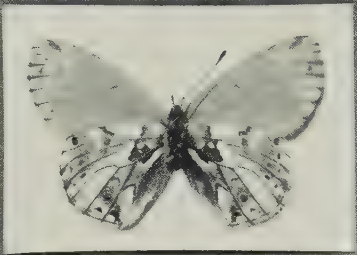
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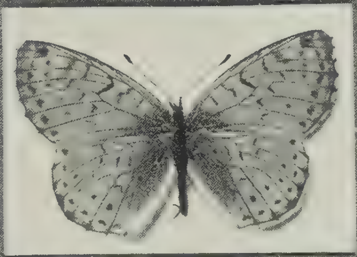
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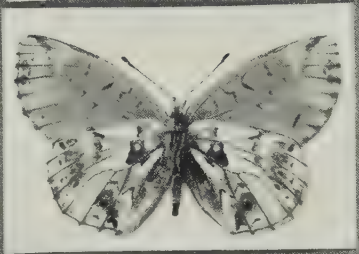
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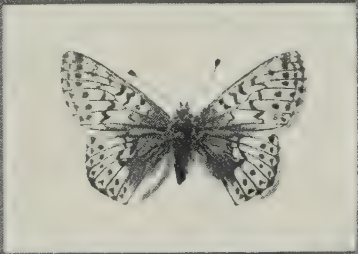
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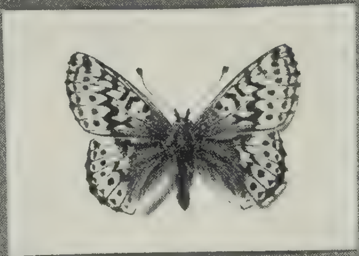
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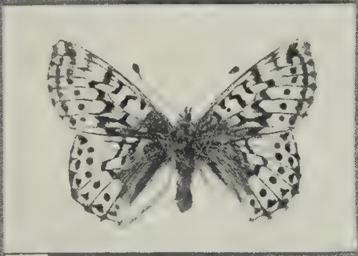
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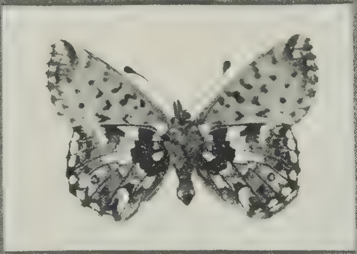
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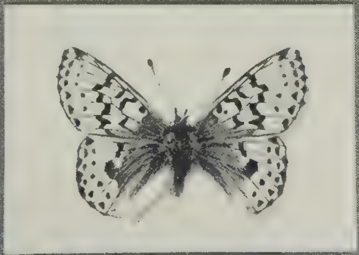
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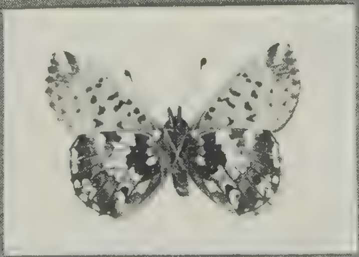
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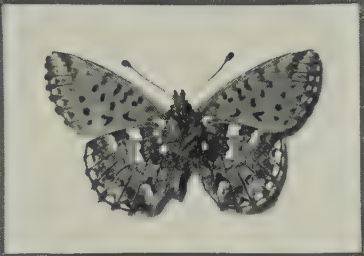
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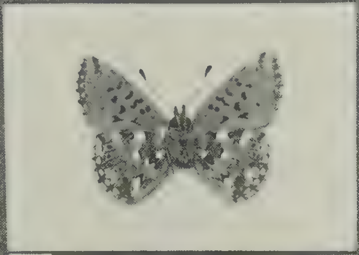
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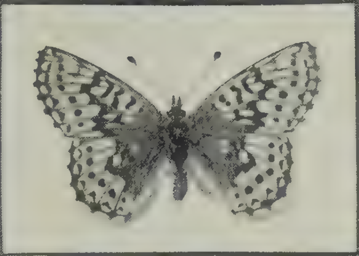
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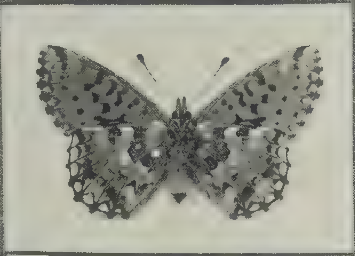
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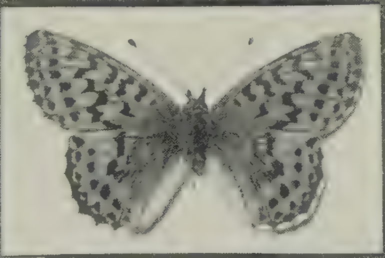
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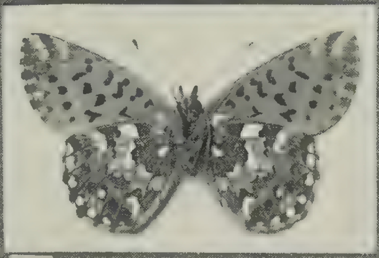
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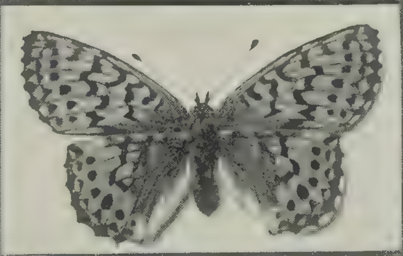
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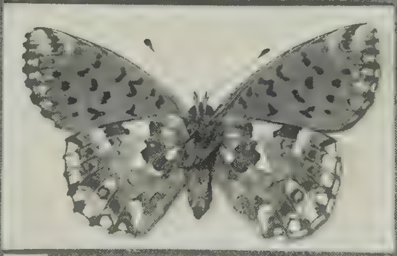
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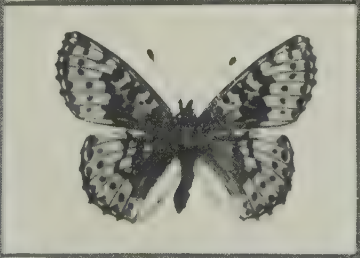
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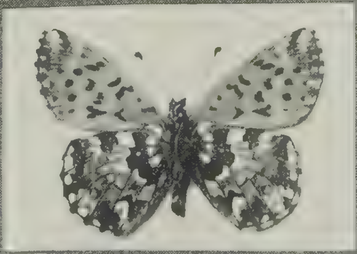
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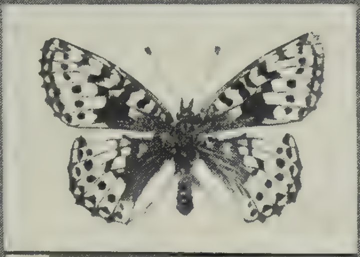
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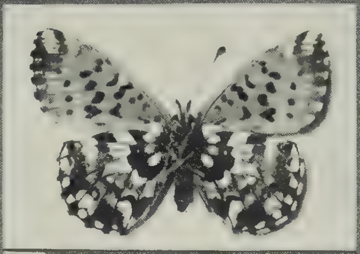
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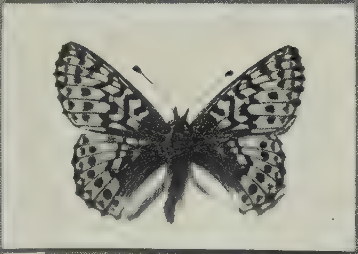
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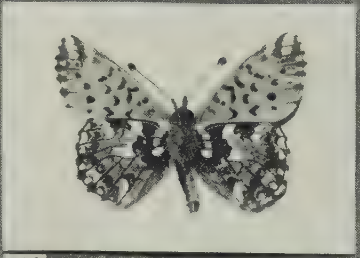
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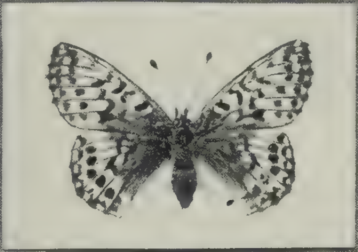
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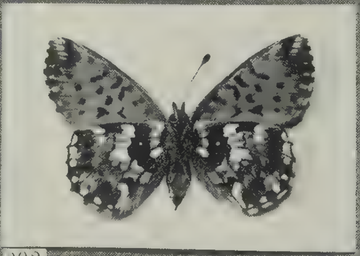
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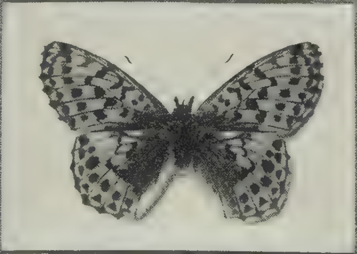
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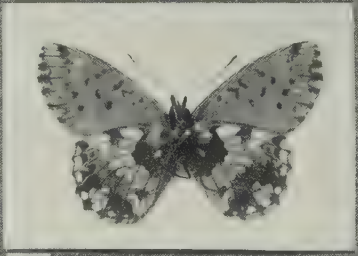
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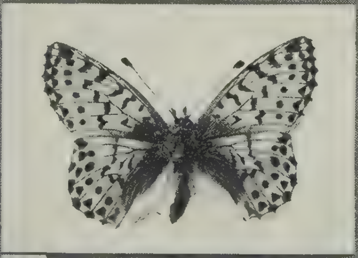
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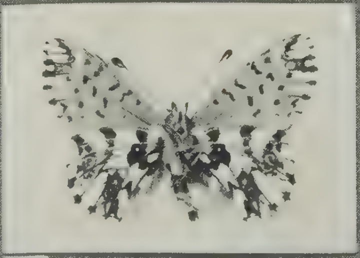
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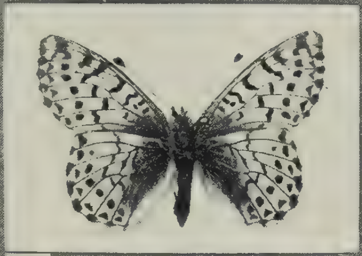
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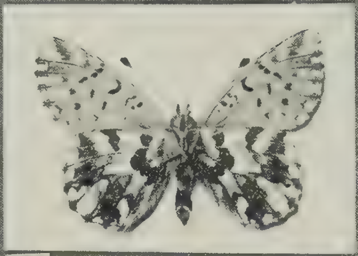
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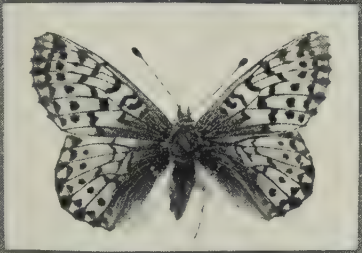
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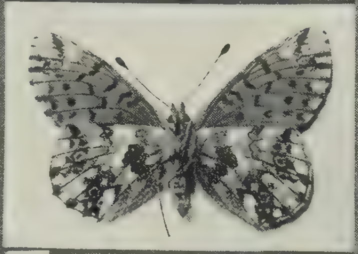
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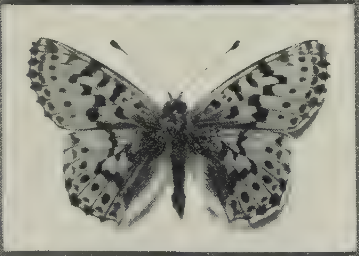
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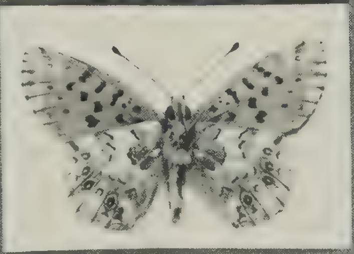
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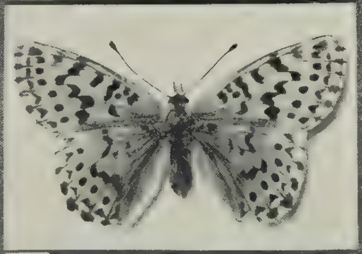
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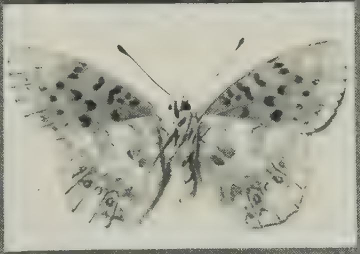
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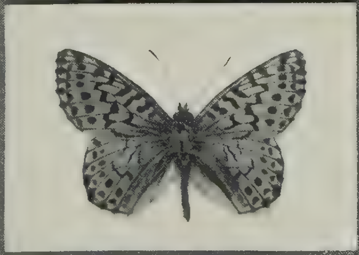
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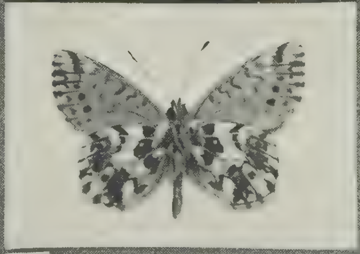
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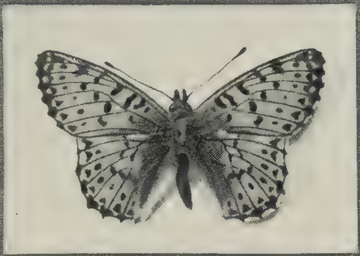
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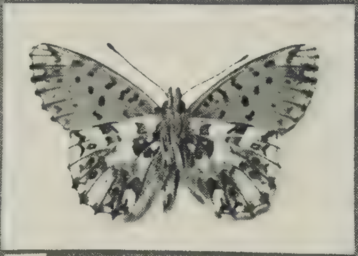
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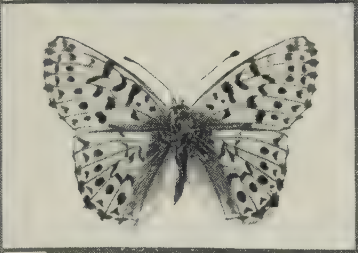
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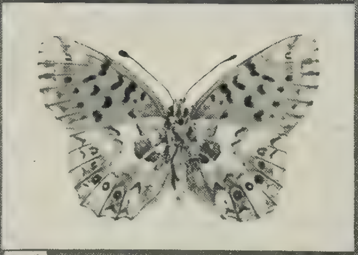
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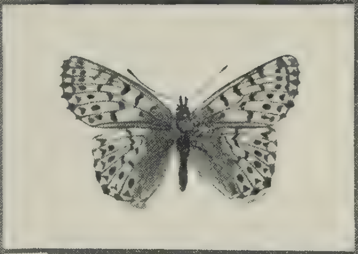
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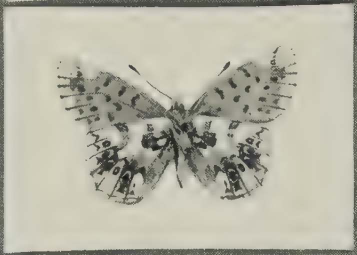
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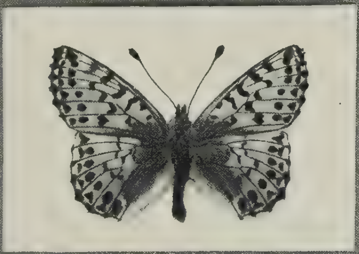
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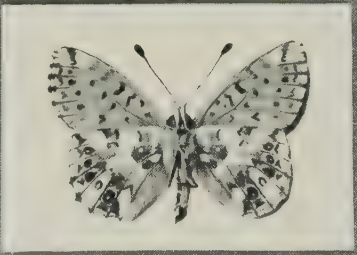
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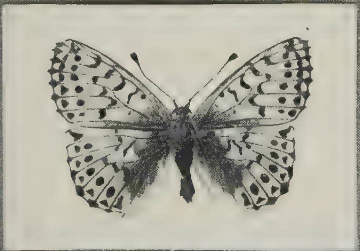
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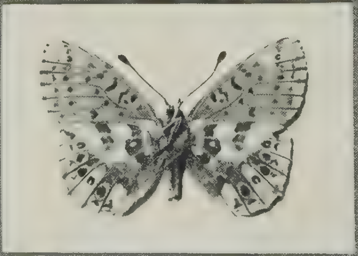
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Review of the classification of the Argynnidi.

THE STRUCTURE AND MECHANISM OF THE SPIRACULAR REGULATORY APPARATUS IN ADULT DIPTERA AND CERTAIN OTHER GROUPS OF INSECTS

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(*Zoological Laboratory, Cambridge.*)

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With 22 Plates and 14 Text-Figures.

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INTRODUCTION.

THE existing literature on the so-called tracheal closing apparatus in insects is neither extensive nor accurate. This may be largely explained, as Babák (1921) has pointed out, by the difficulties encountered in experimental investigations of these very small structures. Most investigations have been carried out on poorly fixed material. Earlier conclusions as to the function of the musculature and the working of the "closing apparatus" are thus largely hypothetical.

The importance of the regulatory mechanism is evident, both in gaseous exchange and in the diffusion of water vapour. The absence of this regulatory mechanism was shown by Ramsay and Manton (1937) to be a possible limiting factor in the evolution of the Onychophora. They concluded that although the Onychophora have developed many features common to successful land animals, their possession of a large number of spiracles without a closing device, and their consequent inability to control their water loss might alone account for their restricted habitat.

In contrast to Onychophora, most insects are able to control these two important processes: (1) the exchange of gases, and (2) the conservation of water, by means of what is called the "tracheal closing apparatus." This apparatus, which is situated at the primary or secondary tracheal orifice, regulates the size of this orifice and thus controls the inward diffusion of oxygen to the tissues, and also to some extent the outward diffusion of carbon dioxide. It also makes possible the conservation of water necessary for the vital activities of the living protoplasm.

It is legitimate to suppose, therefore, that the successful evolution of insects as a group of terrestrial organisms has been largely facilitated by the presence of the "tracheal closing apparatus."

From the economic standpoint, the study of the "closing apparatus" may yield information which will be of assistance when applying fumigants to insect pests: the dose may be fixed according to the type of "closing apparatus" the insect possesses. Other conditions being equal, the dose of gas given to those insects with an efficient type of "closing apparatus" must be greater than that given to those in which this structure is absent or feebly developed.

The title of this paper needs some explanation in that the term "spiracular regulatory apparatus" is used instead of the term "tracheal closing apparatus" adopted by Landois and Thelen (1867). This latter term has been discarded for the following reasons: (*a*) the apparatus is situated either externally at the spiracular opening, or internally, at or just above the tracheal opening, and not at the tracheal opening only, as the older term implies; (*b*) morphologically, the apparatus is more akin to the spiracle itself than to the tracheae; (*c*) primitively, it was situated at the spiracle itself and only later was it carried inwards; (*d*) its function, as Babák (1921) and Snodgrass (1935) have remarked, is not merely to close the trachea, but also to regulate the size of the main pathway to the tracheal system.

The term "lip" used by various authors has been replaced by "lid" owing to the fact that the lids cover the spiracular opening after the manner of "eye-lids," and show, when regulating the size of the opening, movements similar to the latter. The spiracular lids may be defined as movable parts of the body wall marked off by the peritremal sclerite. Their shape varies in different insects. When they are situated at a lower level than that of the surrounding integument, they exhibit some modification in their structure and texture. For these the term "membranous flaps" has been adopted since they are always of a thin elastic membranous nature and often show markings similar to those of the vestibular wall.

The work described below is concerned with the Thysanura, Mecoptera, Neuroptera, Trichoptera, and mainly with Diptera: the Diptera because they constitute a hitherto comparatively untouched field, the Mecoptera, Neuroptera and Trichoptera because of their relationship with the Diptera in the Panorpoid Complex of Tillyard, the Thysanura because they offer the possibility of tracing the evolution of the regulatory apparatus and of studying the relation between the environment and the degree of development of the apparatus.

ACKNOWLEDGEMENTS.

It is with great pleasure that I express my indebtedness to my supervisor, Dr. W. H. Thorpe, for suggesting this problem and taking a keen interest in the progress of the work. I wish to express my sincere thanks and gratitude to Dr. A. D. Imms, F.R.S., for his most valuable suggestions. I am also indebted to Professor D. Keilin, F.R.S., for his kind advice, and to Dr. L. E. R. Picken for reading through some parts of the manuscript. My thanks are due to Dr. O. W. Richards of the Imperial College of Science and Technology for identifying my material and to Professor J. Gray, F.R.S., for providing me with every facility for work in the Zoological Laboratory, Cambridge.

REVIEW OF THE LITERATURE.

Since the work on the morphology of the spiracles and the so-called "closing apparatus" in insects has been reviewed and summarised both by Krancher (1881) and by Babák (1921), it need not be described here. A few points, however, are pertinent to the results of the present investigation and a brief outline of these is necessary.

In their important work on the "tracheal closing apparatus" in insects, Landois and Thelen (1867) came to the following main conclusions:—

(1) The parts of the "tracheal closing apparatus" are "chitinous" and consist of (*a*) a closing bridge, (*b*) a closing lever or cone, (*c*) a closing band, and (*d*) a closing muscle. The first three are situated near the beginning of the

trachea, and are flexibly articulated with each other. The closing bridge is semi-lunar and extends round one-half of the tracheal tube, whilst the closing band is a thin chitinous strip placed around the other half opposite to the bridge. The stick-like lever presses the band against the bridge so as to close the tracheae. One muscle only is present and is attached to one end of the lever or the cone, and to the bridge, over which it sometimes passes to terminate on the hypodermis. In cases where two cones are present, the closing muscle is stretched between them.

(2) Closure is effected when the band becomes pressed against the bridge by muscle contraction, the actual mechanism varying somewhat in different insects. Opening is due to the elasticity of the parts of the apparatus.

Furthermore, these two authors named the parts of the highly developed regulatory apparatus, which they first investigated. These names were generally adopted by later workers for analogous parts, although the actual form of the structure might be very different.

Krancher (1881) in general agreed with Landois and Thelen. In some cases, however, he mentioned two muscles as opposed to the single muscle cited by the above-mentioned authors. He discussed the question of the origin of the "tracheal closing apparatus" and maintained that it was merely a locally thickened part of the spiral fibre of the tracheae. This assertion he based on his finding that in the most primitive type of "closing apparatus," such as he thought to exist in the larvae of Diptera, the tracheae bordering the opening are surrounded by a ring consisting of several layers of "chitin," resembling a thickened spiral fibre. This he said can also be demonstrated in more highly developed and complicated apparatus, in which the closing bridge is seen to be formed by a number of single spirals fused together. Through increased "chitinisation" the closing levers and cones appeared. According to Alt (1909) and to Mammen (1912), the "closing apparatus" is formed from "chitinised" parts of the stigmatic cavity. The more recent work on the "closing apparatus" is mentioned in the relevant sections of the following account.

MATERIAL AND TECHNIQUE.

The adults of most of the insects investigated were secured from the Cambridge district and kept alive for some time in the laboratory. A few insects were bred in the laboratory and their larval forms were examined. The insects were first examined under the binocular microscope and then killed in various ways so that the parts of the regulatory apparatus could be seen in as many positions as possible: thus a more correct interpretation of the mechanism involved during its opening and closing could be deduced. Chloroform, ether, decapitation, shaking and heating were tried. In addition, insects which had died "naturally" were examined. Bleaching was found necessary for the heavily pigmented insects. For this, insects or parts of insects were left to bleach in chlorine vapour in small jars for between half an hour and two hours, the period depending on the degree of pigmentation of the integument.

In order to be sure of the uniformity of the abdominal regulatory apparatus, each of the abdominal spiracles was examined separately in all the cases investigated.

The material was examined by the following methods: (*a*) observations on living or anaesthetised insects under the binocular microscope, (*b*) dissection, (*c*) stained whole mounts, (*d*) unstained whole mounts for examination with polarised light, and (*e*) serial microtome sections.

(*a*) As some of the thoracic spiracles possess an external regulatory apparatus, it was necessary to investigate the mechanism of regulation in living or anaesthetised insects. For this purpose the insect was placed on the binocular stage and forced to move its legs for some time in order to increase the rate of gaseous exchange. Soon after, the thoracic spiracles were seen to open and close rhythmically, rapidly in the beginning and then more slowly. In this way it was possible to study the movement of the spiracular lids.

(*b*) For dissection the material was fixed in 70% alcohol or Pampel's Fluid. In most cases it had to be hardened by leaving the material in 70% or 90% alcohol for 12 to 24 hours. The specimens were then stained either in borax carmine or haematoxylin. The body muscles were carefully separated, leaving the musculature of the regulatory apparatus intact. It was then possible in some cases to observe the mechanism of regulation in both the thoracic and abdominal spiracles by pressing with a fine needle on the muscles wherever their size permitted and noticing the movement of the parts.

(*c* and *d*) For whole mounts the material was fixed in hot 70% alcohol, after which it was hardened and stained as in (*b*). The regulatory apparatus was then dissected out and mounted in Canada balsam. The same method was used for whole mounts to be examined by polarised light, except that these were left unstained. In the majority of cases the polarising microscope was found to be necessary especially when the minute size of the muscles of the apparatus rendered their differentiation after staining difficult. In the dark field of the polarising microscope the fibrous tissue as well as the musculature can be distinguished very clearly.

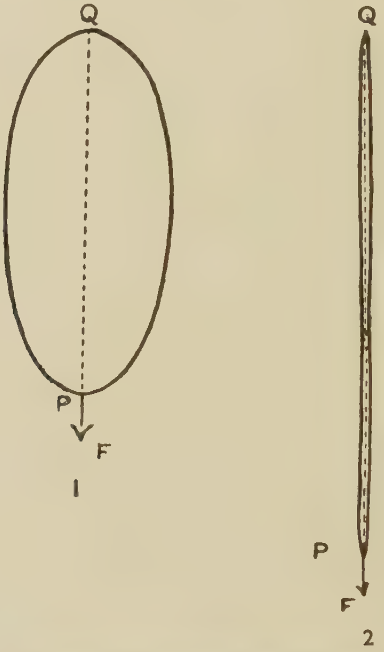
(*e*) For section cutting the most satisfactory method was to fix the material in alcoholic Bouin's fluid and afterwards stain with Mallory's triple stain. The specimens were left in the fixative for 12 hours, then washed in four changes of 80% alcohol for 2 hours. They were transferred to 90% alcohol for one hour and then to two changes (12 hours each) of methyl benzoate containing 1% celloidin. This was followed by two changes of benzole, 20 to 30 minutes each and then a mixture of wax dissolved in benzole, and lastly by three changes (2 hours each) of wax.

The illustrations were made with the assistance of a camera lucida.

THE GENERAL MECHANICAL PRINCIPLES OF THE REGULATORY APPARATUS.

The various types of spiracular regulatory apparatus investigated here (with the possible exception of the anterior thoracic apparatus of Neuroptera and the abdominal apparatus of Mecoptera and Neuroptera) all exploit the elastic properties of sclerotised cuticular parts. In all cases closure is brought about by the deformation of certain elastic structures as a result of the contraction of special closing muscles. The potential energy stored in the distorted elastic membranes restores the apparatus to its normal configuration, that is, re-opens the spiracle when the muscle relaxes. The tension set up in the contracting muscle may act directly on the deformable elastic surfaces, as when the muscle is inserted directly on these, or indirectly, when the muscle is inserted on a rigid lever or similar structure, whereby both the direction and magnitude of the deforming force may be changed.

In all the insects studied (except the anterior thoracic spiracles of Neuroptera), the thoracic spiracles possess one muscle, the closing muscle. This acts on elastic folds, mostly in the form of rings or callipers which arise as thickenings of the inner rims of flexible lids or membranous flaps. These folds may be very thin and placed at the proximal end of the atrium, or they may appear as sclerotised bars on either side of its distal part. Great as is the variation in these structures, the mechanical principles involved in opening and closing are the same. The folds can be compared to an elliptical ring of material of high elastic modulus, the shape of which when no external force is acting is as in text-fig. 1. If a force *F*, the direction of which is indicated by the arrow, acts at a point diametrically opposite to the point *Q* at which the ring is fixed, it will set up a longitudinal stress in the elements of the ring, causing it to assume the shape shown in text-fig. 2. Owing to the elastic nature of the ring, potential energy is stored during deformation and serves to re-open the ring when the force *F* ceases to act. As the elastic folds are continuous with the lids or the flaps, their distortion cannot occur without the lids or the flaps also suffering distortion.



TEXT-FIGS. 1 and 2.—Diagrams illustrating the principles involved in a simple type of closing apparatus.

In addition to the rings and callipers other structures, such as sclerotic thickenings of the spiracular lids or the flaps near their rims or at their bases, may be present. These thickenings may be fused with elastic membranes (Brachycera, Cyclorrhapha) to form variously shaped elastic plates embracing the base of the rings and the flaps (that is, the region of the muscle attachment), or connecting the two arms of the calliper together. In such cases the muscle is inserted on the elastic plate which becomes of great importance in the opening and closing of the spiracle.

In the Diptera, therefore, the opening muscle present in the anterior thoracic spiracle of certain insects such as that of the Neuroptera, is replaced by simple but efficient devices : rings, callipers, plates and other structures, the elasticity of which restores the spiracular regulatory apparatus to its resting open configuration when the closing muscle ceases to contract.

In the abdominal spiracles, the muscles act on rigid structures in the form of levers or plates connected with other cuticular elements such as bands, spurs and the like, by means of which the size of the opening leading to the tracheae is regulated. The movement of these rigid structures is facilitated by their flexible or elastic articulations with other parts of the apparatus. The various elements of the regulatory apparatus are joined by connective tissue fibres and elastic membranes. The presence of these indicates the flexibility and elasticity of the apparatus and explains the readiness with which it collapses when the muscle contracts, and dilates when the muscle relaxes. They also assist the musculature of the body wall in maintaining the apparatus in position.

Two types of levers are found : (1) that of the second order where the weight (opening) is situated between the fulcrum (point of attachment of the lever) and the power (the muscle)—this type is mostly found in the Nematocera ; and (2) that of the first order, which is the common type in Brachycera and Cyclorrhapha.

While in the Diptera a closing muscle only is present, in the Mecoptera and the Neuroptera there is an opening as well as a closing muscle. A brief discussion of the mechanics of the spiracular regulatory apparatus in the abdominal spiracles of the Mecoptera will be found in the section dealing with this group.

THYSANURA.

An investigation of the Thysanura was undertaken in order to determine whether the most primitive insects possess any means of regulating the size of the external opening of the tracheal system. It was thought that such a study might throw some light on the nature and evolution of the regulatory apparatus in the higher forms of insects. To this end, *Machilis* sp. and *Lepisma saccharina* among the Ectognatha and *Campodea* sp. and *Japyx*[1] sp. among the Entognatha were examined.

In accordance with the findings of Davies (1927) for Collembola, no regulatory apparatus was found in these forms : in all cases, the spiracles communicate with the exterior by simple openings without any provision for the regulation of their size. The illustrations in Plate I show that both thoracic and abdominal spiracles are bounded by a cuticular ring (pl. I, figs, 2, 3 and 4 : R) and lead directly to the tracheal system.

The absence of regulatory apparatus in the Apterygota suggests that the problem of water conservation is not an important one for these forms, which, indeed, as a rule, occur in situations where moisture is abundant and the relative humidity high, as in the soil under leaf deposits or under stones (Imms, 1934). It is interesting to note that in *Lepisma saccharina* a few strands of muscle were found around the spiracular opening.

Connective tissue (pl. I, fig. 4 : CT), containing both "white" and "elastic" fibres is of common occurrence around the spiracular openings. The fibres are found in the immediate neighbourhood of the cells that lay down the tracheal cuticle. Compared with the neighbouring tracheal cells, those associated with connective tissue fibres are less regular in shape and in closer contact. In *Machilis* (pl. I, figs. 1 and 2) it was found that elastic fibres predominate in the connective tissue, whereas in *Lepisma* (pl. I, fig. 4) fibrous tissue seems to be more common.

The theory that the tracheal epithelial cells may be responsible for the production of the connective tissue surrounding the spiracular openings or investing the spiracular regulatory apparatus is supported by the work of Dreher (1936) on the honey bee. This author found that the spindle-shaped cells, described by Trapmann, Weil and others as forming connective tissue and elastic membranes, are identical with the dense network of tracheal end-cells and tracheal capillaries found by him and by Morrison on the midgut of the honey bee. He concludes, therefore, that the ramified tracheal end-cells form a tissue functionally comparable to the connective tissues of other animals.

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[1] Indebtedness is due to Dr. A. D. Imms, F.R.S., for two specimens of *Japyx* sp. (1·25 cm. and 2·65 cm. long respectively) from South Africa.

The apparent formation of a fibrous connective tissue from tracheal epithelial cells, found by the writer, or from their homologues (Dreher, 1926, and Wigglesworth, 1939) is not in accordance with Lazarenko's (1925) theory that such tissue is derived from the wandering blood cells.

MECOPTERA.

Panorpidae.

Panorpa communis L.

Landois and Thelen (1867) in their treatise on the " tracheal closing apparatus in insects " briefly mentioned, without figuring, the " closing apparatus " found in the abdomen of *Panorpa communis* (this species was included by them, as well as by Krancher (1881), under Neuroptera).

Krancher (1881) attempted to give a more detailed description of the thoracic as well as of the abdominal " closing apparatus " of *Panorpa communis*. But he, as well as the first two authors, was unable to deduce correctly the functioning of the parts of the apparatus on account, among other things, of his superficial study of its morphology. Krancher, moreover, did not figure any of the thoracic spiracles, and he mistook the first abdominal for the second thoracic, the latter being overlooked altogether. Describing the abdominal spiracles, Krancher stated that, with the exception of their smaller size, they are similar to the second thoracic (first abdominal).

The following work was carried out on *Panorpa communis* L. An account of the morphology of the thoracic and abdominal spiracles is first given, then in each case there follows a description of the mechanism involved in opening and closing the main pathway to the tracheal system.

The Thoracic Spiracles.

The anterior thoracic spiracle (pl. II, fig. 1) is by far the largest of all the spiracles. It lies in the yellowish intersegmental membrane between the pro- and meso-thorax, with its upper edge at the tergo-pleural suture. The spiracular opening (O) is marked with an oval blackish sclerotic ring (R) which merges into the spiracle lids (LD). The latter are overgrown with rows of hairs, parallel to the fissure of the spiracle. None of these hairs projects over the opening to collect the dust as Krancher stated. There is no peritreme and the slightly brownish spiracular lids gradually pass into the body wall which is little lighter in its colour than the lids themselves. Beyond the spiracular opening there is a narrow semi-oval atrial chamber which arises from the internal surface of the lids and opens at the other end to the trachea. A strong closing muscle (CM) which originates on an apodemal ridge is inserted with its narrow end on the base of the ring.

The " closing apparatus " as described by Krancher (1881) is at the place where the atrium becomes very narrow and the transition into the trachea takes place. There is, he said, a chitinous rod on either side of the tube, these being connected below at the point where the closing muscle is inserted. According to him, contraction of the muscle brings together the two chitinous rods, and in doing so squeezes the trachea which lies between them.

It appears from Krancher's description, therefore, that the anterior thoracic spiracle of *Panorpa* possesses an internal type of apparatus situated at the tracheal mouth and acting directly on it, thus regulating the passage to the trachea. During the present investigation, however, it was found that the anterior thoracic spiracle of *P. communis* has an external or lid type of regulatory apparatus consisting of the following parts: (*a*) the lids, (*b*) the ring, and (*c*) the closing muscle. Contraction of the muscle draws the two sides of the ring together. The latter, acting on the stigmatic lids, forces them to approach each other by an upward movement until they meet, then their edges bend inward, thus closing the fissure between them. During this action, as observed in the living insect under the binocular, it is the external opening lying between the spiracular lids that is closed, not, as Krancher thought, the tracheal mouth. In fact the latter remains widely open whether the external opening is opened or closed.

As soon as the muscle relaxes, the lids separate by reversal of their movement, thus leaving the opening free.

The posterior thoracic spiracle is placed in the intersegmental membrane between the meso- and metathorax, with its longitudinal axis lying vertically to that of the body wall. It is about half the size of the anterior thoracic, and twice as large as the first abdominal spiracle. The spiracular lids (LD) are of unequal size, the anterior being somewhat thicker and larger than the posterior, and is covered with a few rows of short thick hairs similar to those of the anterior spiracle. Those bordering its outer rim are longer than the rest. The posterior lid, which is partly overlapped by the anterior, is devoid of hairs and is a little paler. This breaks the outline of the spiracle and makes it difficult to see, especially if it is closed, since its colour is almost the same as the surrounding body wall. A fan-shaped closing muscle (CM) which has its broad base on an apodemal plate (PL) is inserted on the ventral part of the lids. This muscle is of considerable length and is mostly inserted on the larger anterior lid which thus becomes the more effective in regulating the spiracular opening.

The regulatory apparatus consists of: (*a*) the lids, and (*b*) the closing muscle. On muscle contraction, the anterior lid approaches the posterior lid by an upward curved movement. The posterior lid moves but very slightly during regulation of the size of the spiracular opening. Owing to the elastic nature of the lids, they move away from each other as soon as the muscle relaxes, and leave the opening free.

The Abdominal Spiracles (pl. II, figs. 3, 4, 5, 6A and 6B).

The abdominal spiracles are oval in shape with their longitudinal axis lying vertically on the body wall. Their size decreases towards the posterior end of the abdomen. The first abdominal spiracle was found to be the most convenient in size for examination and so is taken as representative of the abdominal spiracles. In the other pairs of spiracles the regulatory apparatus is of the same type, save that it is very feebly developed in the last three in accordance with the size of the spiracles.

The spiracular opening (pl. II, fig. 3: O) is oval and guarded by a sclerotised blackish peritreme (PR), consisting of two well-defined halves. The posterior portion is thin and in the form of a half oval; the anterior part is thick and heavily pigmented and is inflected inside the body so as to provide a firm base for the regulatory apparatus (the bridge). Rows of long hairs arise from the latter portion of the peritreme, and being directed towards the opening, as mentioned by Krancher (1881), form an efficient filter apparatus. A few short hairs arise from the posterior part of the peritreme.

The "closing apparatus" as described by Landois and Thelen (1867) consists of: (*a*) the closing bridge, (*b*) the closing lever, and (*c*) the closing muscle. In addition to these a band, a membrane and an opening muscle were found during the present work.

A large lever (L) arises from the uppermost part of the peritreme at the point where the posterior thin half emerges into the thick anterior part. The lever's head, which is continuous with a flexible articulation with the peritreme, is elongated from one side into a thin band (BD). The latter borders an elastic membrane (pl. II, figs. 3, 4, 6A and 6B: MB), stretched between the posterior part of the peritreme and the band, and covers the tracheal mouth. Two muscles are attached to the free end of the backwardly directed lever. The first is a short closing muscle (pl. II, figs. 3, 5, 6A and 6B: CM) inserted with its narrow end on the lower part of the bridge opposite the lever's head. The second is a long opening muscle (OM) which is more or less in a line with the occlusor and takes its origin at the tergo-pleural suture.

During dissection the regulatory mechanism was examined by pressing very lightly with a fine needle on the closing muscle whenever the apparatus was in the open condition. In so doing the lever, which is placed at about 120° to the band, swings downwards and draws the membrane over the tracheal orifice until the band comes against the thick inflected part of the peritreme and closes the tracheal mouth. In the closed position the lever is at about 90° with the band (pl. II, fig. 6B). On releasing the pressure, the lever, together with the band and the membrane, go back to their previous positions, leaving the tracheal mouth free (pl. II, fig. 6A). In cases where the apparatus is in the closed condition, pressing on the opening muscle results in slight and incomplete opening of the tracheal mouth.

The above observations, together with those made on a large number of whole mounts and sections in both the opened and closed condition, show that when the closing muscle contracts it imparts a slight twist to the end of the lever which is attached to the muscle. This twist affects the lever's head which is then pushed against the opposite side. Hence the band comes against the bridge, and the membrane stretches over the tracheal mouth. On relaxation of the occlusor and contraction of the opener the lever's head is pushed away from the bridge. Thus, the band and the membrane go back to their previous positions, leaving the tracheal opening free. It would appear from their description and figures that Landois and Thelen (1867) and Krancher (1881) overlooked the opening muscle and assumed that the opening of the tracheal mouth is wholly achieved through the elasticity of the parts of the apparatus.

NEUROPTERA.

Sialioidea.

Sialis lutaria L.

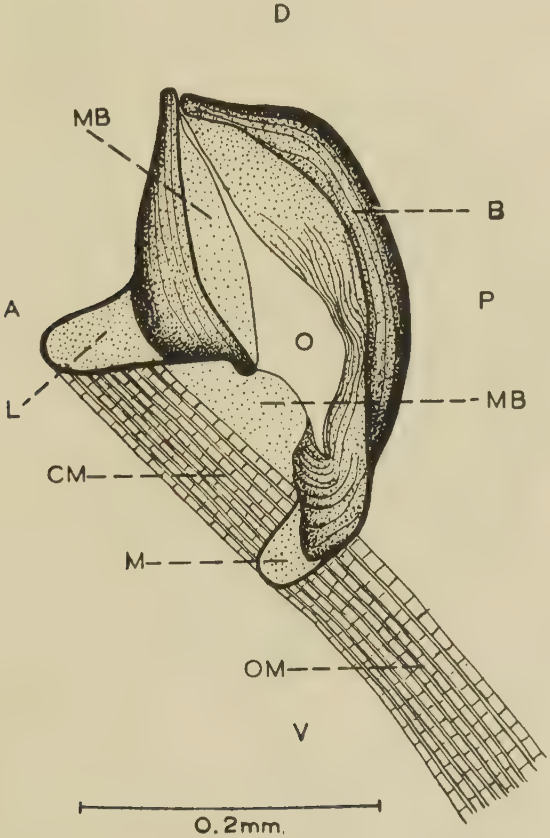
Krancher (1881) referred to *Rhaphidia* as possessing a "closing apparatus" similar to that of *Panorpa communis*, differing only in the shape of the lever which is in *Rhaphidia* like a triangular plate. Mammen (1912), working on

Hemiptera, gave two figures for an anterior thoracic and an abdominal spiracle of *Chrysopa* sp.

In this work *Sialis lutaria* was investigated and it was found that, unlike *Panorpa communis* but like *Limnophilus* sp. described below, the thoracic spiracles possess two different types of regulatory apparatus.

The Thoracic Spiracles.

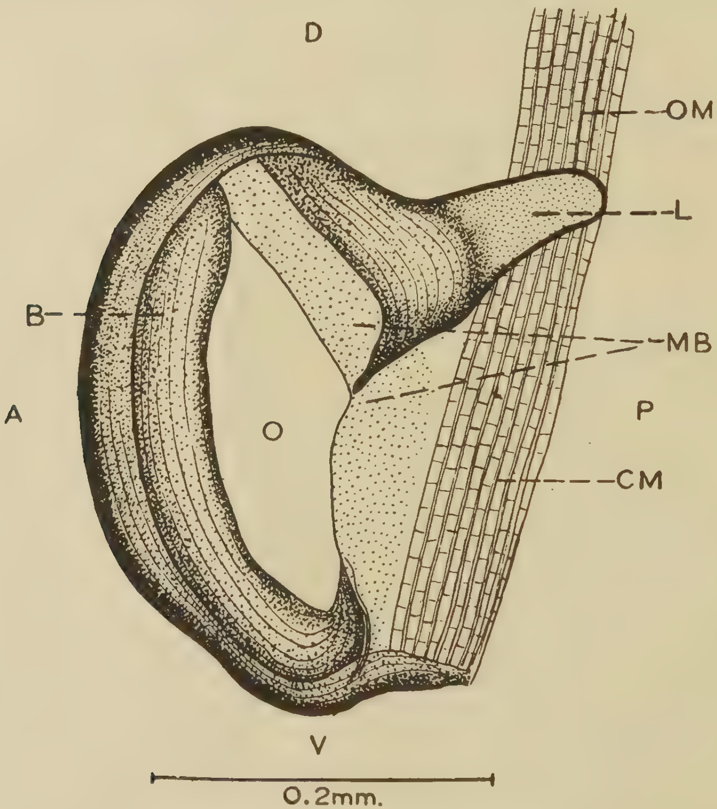
The anterior thoracic spiracle (text-fig. 3) lies in the intersegmental membrane between the first two thoracic segments. Posterior to the spiracular opening (O) is a sclerotic plate which is inflected inside the body to form a bridge (B), composed of two parts, a thick dark margin and a rather broad yellow region. The ventral edge of this plate is produced into a process or manubrium (M) to which a closing and an opening muscle are attached. Situated opposite the bridge and anterior to the spiracular opening is a large two-headed lever (L), flexibly articulated with the uppermost end of the bridge. There are two muscles for regulating the spiracular opening : an occlusor (CM) and an opener (OM). The occlusor runs from the lever to the manubrium, and the opener, which is a much longer muscle, is in a line with it, lying between the manubrium



Text-fig. 3.—First thoracic spiracle of *Sialis lutaria*, in the open position.

and the pleural wall. An elastic membranous part (MB) of the pleural wall is stretched between the two heads of the lever and the manubrium.

The regulatory apparatus consists, as in the abdominal spiracles of *Panorpa*, of the following parts : (*a*) the bridge, (*b*) the lever, (*c*) the elastic membrane, (*d*) the closing muscle, and (*e*) the opening muscle. On contraction of the occlusor and relaxation of the opener, the lever moves downwards and the manubrium upwards so that the broad parts of the lever and the membrane are pushed against the yellow inner part of the bridge. This causes the membrane to cover the spiracular opening.



Text-fig. 4.—First abdominal spiracle of *Sialis lutaria* in the open position.

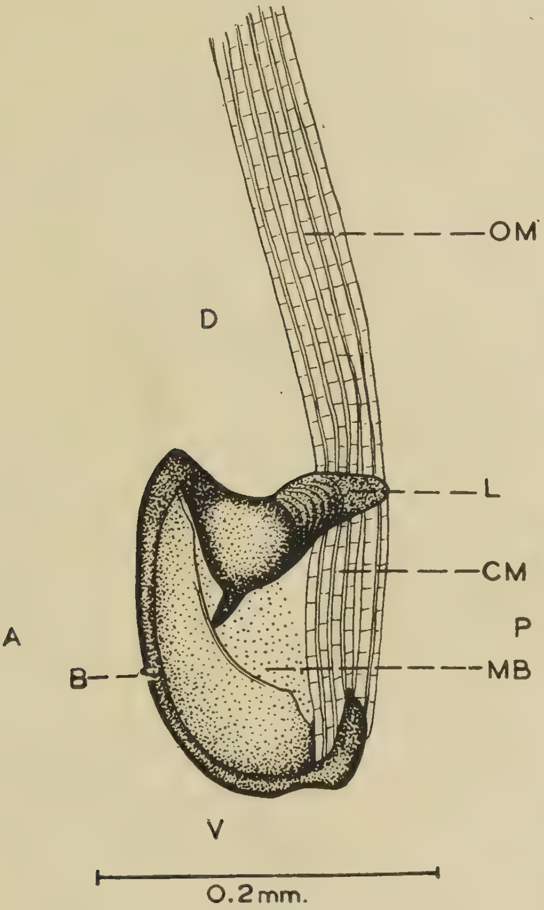
The posterior thoracic spiracle is placed in the intersegmental membrane between the basal articulations of the second and third leg. It is oval in shape and larger than the anterior thoracic spiracle. The structure and mechanism of the regulatory apparatus is as described above in the posterior thoracic spiracle of Mecoptera (p. 111).

The Abdominal Spiracles.

These are oval fissures situated in the middle of the pleura. As in Mecoptera, the first is the largest and is therefore more easily examined.

As seen from text-figs. 4 and 5, and also from Mammen's figure (35) of *Chrysopa* sp., these stigmata closely resemble those of *Panorpa* (vide pl. II, fig. 3).

The mechanism regulating the spiracular opening, and the mechanical principles involved, are exactly the same as in Mecoptera, and the regulatory apparatus consists essentially of the same five parts. The opening muscle was neither mentioned nor figured by Krancher (1881).



TEXT-FIG. 5.—An abdominal spiracle of *Sialis lutaria* closed.

TRICHOPTERA.

LIMNOPHILIDAE.

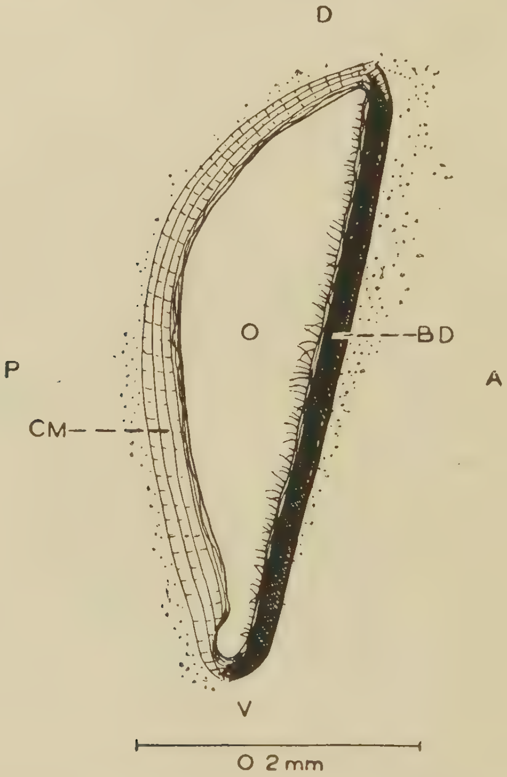
Limnophilus sp.

The order Trichoptera is mentioned in Mammen's work (1912) on Hemiptera in which one figure, depicting the first thoracic spiracle of a trichopterous insect, is given.

In the present investigation, *Limnophilus* sp. has been studied as a representative of this order.

The Thoracic Spiracles.

The anterior thoracic spiracle (Mammen, 1912, fig. 32) is an oval slit in the intersegmental membrane between the pro- and mesothorax with its dorsal end at the edge of the tergal plate. The body wall around the spiracular opening forms an oval margin which is inflected inwards and merges into the tracheae. From the internal surface of this margin arise a few rows of long hairs which protect the tracheal entrance. The spiracular opening is further guarded by a tuft of hairs which extend backwards from the base of the first leg. A strong spindle-like closing muscle composed of a large number of bundles of fibres extends along the anterior margin of the spiracle close to the tracheal entrance. This muscle is attached to a cuticular process at the ventral edge of the spiracle, while its narrow end is fastened to the pleuron near the dorsal end of the spiracular opening. The closing muscle acts directly on the tracheal entrance in a region devoid of taenidia. Its contraction causes the anterior half of the tube, close to the muscle, to be brought against the opposite side, thus closing the tracheal entrance. Owing to the elasticity of the membranous part of the tracheal entrance, direct communication with the outside air is established as soon as the muscle ceases to act.



TEXT-FIG. 6.—First abdominal spiracle of *Limnophilus* sp.; internal view open.

The posterior thoracic spiracle is an oval opening lying in the intersegmental membrane between the meso- and metathorax. As in Neuroptera, this spiracle is much larger than the anterior thoracic, and is covered with two lids, from which fine hairs project over the tracheal opening.

The structure and mechanism of the regulatory apparatus is similar to that described above in Mecoptera (pp. 111, 112).

The Abdominal Spiracles (text-fig. 6).

These are small semi-lunar openings covered with a few very short hairs arising from their anterior borders. The first abdominal is by far the largest of all and is therefore the most suitable for investigation.

This spiracle is placed directly behind the thorax in the anterior portion of the first abdominal segment. The straight anterior margin of the spiracle is bordered by a brown sclerotic arm or band (BD) extending along the pleural wall, and provides a firm base for the regulatory apparatus (the bridge). The semi-lunar posterior margin is inflected inwards where it merges into a very narrow membranous region at the tracheal entrance. The closing muscle (CM) is slender and is composed of a few bundles, each consisting of a small number of fibres. It is tightly applied to the inner inflection of the posterior dorsal and ventral edges of the spiracle and consequently assumes a curved form.

The regulatory apparatus is very simple, possessing no specially developed parts like those found in Mecoptera and Neuroptera. The closing muscle acts directly on the elastic internal inflection of the semi-lunar margin of the spiracle, which, on muscle contraction, is brought against the anterior margin and thus closes the tracheal opening. When the muscle relaxes, the posterior margin, by virtue of its elasticity, goes back to its original position and leaves the tracheal opening free.

The above accounts of Mecoptera, Neuroptera and Trichoptera show that there is great similarity in the structure and mechanism of the second thoracic and abdominal regulatory apparatus of the first two orders. The second thoracic spiracle of *Limnophilus* agrees with that of Mecoptera and Neuroptera, but the anterior thoracic as well as the abdominal spiracles are different; their regulatory apparatus is more generalised.

DIPTERA.

Nematocera.

Chironomidae.

Chironomus dorsalis Fab.

The Thoracic Spiracles.

The anterior thoracic spiracle (pl. III, fig. 1) is oval and is situated on the intersegmental membrane between the first and second limb bases. It is a little larger than the posterior spiracle and its dorsal end is directed slightly towards the head of the insect. The thin peritreme (PR) demarcating the spiracle is darker than the rest of the surrounding pleural area, and arising from its edge are long unbranched hairs which form a somewhat funnel-shaped hairy cover to the opening. Those arising from the anterior and ventral edges of the peritreme are longer than the rest. Two membranous flaps (MF) are placed directly beneath the hairy cover. Their opposing rims are thickened to form two bands (BD) which are connected at their bases by an elastic plate (E). A fan-shaped closing muscle (CM) has its broad end partly on a plate-like apodeme (APT) and partly on the pleural wall, and is inserted on the elastic plate. Contraction of the muscle brings the two bands together. These draw the flaps upwards (in the plane of the body wall) and inwards (towards the mid line of the spiracular opening), thus closing the spiracle. Opening is dependent on the elasticity of the bands and their connecting plate, which, as soon as the muscle relaxes, forces the bands away from each other, carrying the flaps back to their original position.

The posterior thoracic spiracle (pl. III, fig. 2) lies beneath the haltere, with its longitudinal axis vertical to that of the body. The oval fissure of the spiracle (O) is covered with fine unbranched hairs of more or less equal length. These hairs arise for the most part from a thin irregular peritreme (PR). A pigmented ring (R) is placed around the tracheal mouth, which lies directly beneath the spiracular opening. The closing muscle (CM), which resembles that of the anterior thoracic spiracle, has its narrow end on the ventral portion of the ring. Its broad base originates on an apodemal plate (APT). As soon as the muscle contracts, the ring pulls the two opposite sides of the tracheal entrance together. On muscle relaxation the ring, owing to its elasticity, separates the two sides of the tracheal mouth once more.

The Abdominal Spiracles (pl. III, figs. 3, 4 and 5).

The abdominal spiracles are placed at the upper edges of the pleura and are covered by the tergal plates. The spiracular opening (O) is a simple minute slit without a peritreme or similar sclerotic structure. It leads into a long tubular atrium devoid of spiral thickenings and guarded on either side by a sclerotic band (BD), the structure of which changes along its length. That part of the band next to the external opening is much more rigid than that which leads to the tracheae, and between these two regions there is a weak flexible point (FP). The long closing muscle (CM) consists of two bundles of fibres running between the two extremities of the atrial tube along one of the bands. It may be mentioned that the two points of muscle attachment correspond with those of the lateral body-wall muscles. For this reason it was difficult to differentiate the fully relaxed muscle from the neighbouring ones. On muscle contraction, the atrial tube is bent in the middle at the flexible region. In the closed position (pl. III, fig. 5), the flexible region, like a bent spring, exerts a tension in the opposite direction to that of the muscle, opening the atrial tube as soon as the muscle relaxes.

PSYCHODIDAE.

Psychoda sp.

The Thoracic Spiracles.

The anterior thoracic spiracle (pl. III, fig. 6) was described and figured by Kemper (1925) in his work on the morphology of the tracheal system of *Psychoda phalaenoides*. His description does not agree in all respects with the state of affairs found in *Psychoda* sp., during this investigation. The anterior thoracic spiracle lies on the anterior part of the pleura of the first thoracic segment, and not on the second thoracic segment as Kemper found in *Psychoda phalaenoides*. The surrounding body wall is transparent and folded internally so as to form a sclerotic horseshoe-shaped plate (PT) (the spring of Kemper), the anterior part of which extends in the form of two arms enclosing an elastic ring (R). The latter is situated just above the tracheal entrance in a region devoid of taenidia. Around the inner edge of the plate is a strong fan-like muscle (CM) composed of a large number of bundles of fibres inserted on the base of the ring. This is not in accordance with the findings of Kemper (1925), who maintained that there are two closing muscles, although in his figure he showed four separate muscles. When the muscle contracts it pulls the sides of the ring together, closing the tracheal entrance.

The posterior thoracic spiracle (pl. III, fig. 7) was briefly referred to by Kemper (1925) as possessing no " closing apparatus." No figures or descriptions were given of it, nor of any of the abdominal spiracles. This spiracle is very minute and lies beneath the haltere, covered with fine hairs. Internally the surrounding pleural area exhibits a thin darkly pigmented fold (F) which thickens and extends from one end to form a strong ridge (RD), supporting a fan-like closing muscle (CM). The narrow end of the latter is partly attached to the lower edge of the fold, but is chiefly fastened to an elastic ring (R). The two ends of this ring do not meet, but pass gradually into a narrow membranous area at the tracheal entrance. Contraction of the muscle occludes the opening by bringing the two sides of the ring together. The elasticity of the ring is sufficient to force open the tracheal entrance as soon as the muscle relaxes.

The Abdominal Spiracles (pl. III, fig. 8).

Except for their smaller size, the abdominal spiracles resemble those of *Chironomus dorsalis* described above. The atrial bands (BD), however, do not show the weak flexible point found in *Chironomus dorsalis*, because they are normally bent in the middle and thus need little force to close the small orifice lying between them.

MYCETOPHILIDAE.

Sciara sp.

The thoracic as well as the abdominal spiracles are very minute, only visible under the high power of the microscope. For this reason the structure and mechanism of the regulatory apparatus has largely been studied in sections.

The Thoracic Spiracles.

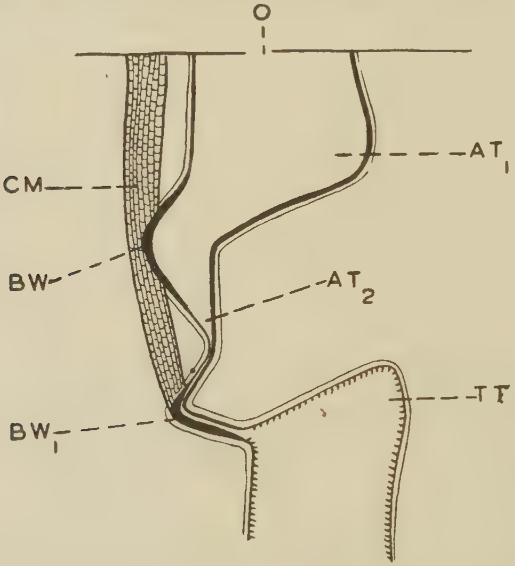
The anterior thoracic spiracle (pl. IV, fig. 1) is situated just behind the base of the first leg. The spiracular area is marked off from the rest of the pleura by a thin peritreme (PR), along the border of which arise some short hairs (H). The spiracular opening (O) is a simple hole, supported at its dorsal end by a slightly sclerotised, n-shaped bow (BW). Directly behind the external opening lies the tracheal mouth, which is marked by a sclerotic fold in the form of a spiral or ring, similar to that of the posterior thoracic spiracle (pl. IV, figs. 2, 3 : F). This ring serves to regulate the size of the tracheal opening. A long closing muscle (pl. IV, fig. 1 : CM), composed of three parallel bundles of fibres, originates on an apodemal ridge (RD) and is attached for the most part to the ventral side of the ring, but also to some extent to the pleural wall, close to the peritremal sclerite. The muscle thus closes the spiracle by deformation of the elastic ring.

The second thoracic spiracle (pl. IV, figs. 2, 3) is flask-shaped, and placed on the pleuron near the third limb base. The simple, minute spiracular opening (pl. IV, fig. 2) lies in a transparent pleural area, the posterior side of which is marked with clusters of short hairs directed towards the opening. It is surrounded by an incomplete sclerotic plate which forms the peritreme (PR). The two sides of the latter are drawn out dorsally into two arms which gradually pass into the integument. As in the anterior thoracic spiracle, the trachea starts directly behind the spiracular opening without the intervention of an atrium, and is marked by a cuticular fold or ring (pl. IV, figs. 2, 3 : F). The short, stout closing muscle (CM) is composed of four more or less parallel bundles of fibres. It arises from an apodemal ridge (RD), and has its insertion mainly on the base of the ring, but to a lesser extent also on the inner surface of the peritreme.

The mechanism involved agrees in detail with that described above for the anterior thoracic spiracle.

The Abdominal Spiracles (pl. IV, fig. 4).

These are small openings situated in the middle of the pleural plates, without any protective structures such as hairs or peritremes. The opening leads into a small sclerotised atrium divided into two parts : an outer dilated chamber (AT_1) and a narrow inner L-shaped tube (AT_2). The latter lies to one side of the chamber, and opens into the tracheae by a small opening (TO), guarded with a few short hairs (H). Along one side of the outer chamber is a sclerotic bow (BW), the proximal end of which marks the beginning of the inner atrial tube. The structure of the latter differs along its length : its proximal section, which forms the outer angle of the L-shaped tube, is produced into a sclerotised bow (BW_1), similar to, and on the same side as that of the outer chamber; while its distal portion, connecting it with the outer chamber of the atrium, is flexible and less pigmented. So there actually are two rigid bows, with a flexible tubular portion between each. This provides a highly efficient arrangement for bending the tube by means of a small force applied at the two rigid points (text-fig. 7). An elongated slender muscle (CM) has its origin on the pleura, close to the spiracular opening. It passes inwards and alongside the bow of the anterior atrial chamber, and is attached to the bow of the inner L-shaped tube. Here again, as mentioned above in *Chironomus dorsalis*



Text-fig 7.—Diagram illustrating the principle involved in the closing apparatus of the abdominal spiracles of *Sciara* sp.

(p. 118), the two insertions of the closing muscle correspond to those of the adjacent lateral body-wall muscles.

BIBIONIDAE.

Bibio hortulanus L.

The Thoracic Spiracles.

The anterior thoracic spiracle (pl. V, fig. 1) is triangular in shape and lies at the upper edge of the pleuron near the base of the first leg. Its narrow dorsal end is directed obliquely towards the head of the insect. The lids of the spiracle (LD) are of equal size, but the antero-ventral lid slightly overlaps the postero-dorsal at the base. Both lids are furnished with rather thick unbranched hairs (H), some of which project over the spiracular opening. The pleural area close to the lids is similarly covered with short hairs in groups of three or four. There is no definite peritremal sclerite, but at the antero-dorsal rim of the opening there is an inverted V-shaped sclerotic fold (F). A broad, fan-like closing muscle (CM) arises from an apodemal plate (APT) of the pleural wall. Its narrower end is partly attached to the basal connection of the spiracular lids and partly to a slightly sclerotic ridge of the pleura close to the base of the lids. The movement of the lids can be followed in half-anaesthetised insects. When the muscle contracts, the lids approach each other, sliding upwards and then inwards towards the mid line of the opening. At the end of this movement, the anteroventral lid slightly overlaps the postero-dorsal, tightly occluding the trachea. As soon as the muscle relaxes, the lids, owing to their elastic nature, separate with an outward and downward movement. It may be noted that the pleural area close to the lids shows slight movement during the opening and closing of the spiracle.

The posterior thoracic spiracle (pl. V, fig. 2) is a long fissure lying at the base of the haltere with its dorsal end inclined slightly backwards. Its shape differs considerably from that of the anterior spiracle, the two lids being narrower and strengthened at their inner edges by a sclerotised ring (R). The lids, which are of equal size, are covered by long, branched and unbranched hairs (H) arising from the edges of a thin peritreme (PR) and from the surrounding pleural area. Around the spiracle the darkly pigmented pleura is swollen to form a ridge guarding the spiracle. This ridge is inflected inwards, forming an apodemal plate (APT) from which a fan-shaped closing muscle (CM) arises. The closing muscle is inserted with its narrow end on the base of the lids and, by its contraction, brings together the lids in the same manner as in the anterior thoracic spiracle (described above). Thus the external opening is tightly closed as soon as the two sides of the sclerotised ring come together.

Opening takes place in exactly the same way as in the anterior thoracic spiracle, but here the rigid pleural area around the spiracle does not move with the lids during opening and closing.

The Abdominal Spiracles (pl. V, figs. 3A, 3B, 4A and 4B).

The abdominal spiracles are slightly oblique slits (pl. V, fig. 3A : O) placed at the middle of the pleural plates. They are more or less of equal size and are guarded by a few hairs (H) directed towards the middle of the opening. There is no well-defined atrium, and the invaginated pleuron leads directly to a narrow tracheal opening (pl. V, fig. 4B : TO) guarded by two bands (BD) situated opposite each other and ensheathed in a dense mass of connective tissue fibres and elastic membrane (pl. V, figs. 4A and 4B : CT). The tracheal mouth and the surrounding tissue are enclosed between the two arms of a large, slightly convex, semi-lunar sclerotic plate (pl. V, figs. 3A, 3B, 4A and 4B: PT) which, owing to its dark colour, can be seen through the transparent body wall. This plate has a thickened, heavily pigmented edge contrasting in colour and texture with the rest of the plate which is thinner, more elastic and paler. The middle portion of the plate is attached to the pleural wall, close to the outer opening, while the two arms (pl. V, figs. 3A, 3B and 4A : L) are more or less free in the body cavity, surrounded only by the musculature of the body wall. Between the free ends of the arms runs a strong closing muscle (CM), composed of a number of more or less parallel bundles of fibres.

The regulatory apparatus consists of : (*a*) two levers formed by the arms of the semi-lunar plate, (*b*) two sclerotic bands situated at the tracheal mouth, and (*c*) the closing muscle. As the muscle contracts, two bands of this nutcracker-like mechanism occlude the opening (pl. V, fig. 3B). The elasticity of the semi-lunar plate plays an important part in the opening of the apparatus. In the closed condition, the plate is bent against the body surface, so that it is in a condition of strain. When the muscle relaxes, the bands separate and leave the trachea open.

A similar type of apparatus has been described by Wigglesworth (1935) in the flea, *Xenopsylla cheopis*. The main difference is that in the latter, in contrast to *Bibio hortulanus*, the apparatus is situated on the tracheal tube which lies in a deep groove in the concave surface of a crescentic rod of chitin—whereas in *Bibio* it is placed at the tracheal mouth which, as in the case of *Xenopsylla*, lies in a groove between the two arms of the sclerotised semi-lunar plate (equivalent to the rod of Wigglesworth). In both cases the two ends of the rod and the semi-lunar plate are connected with a closing muscle, the contraction of which results in the occlusion of the tracheal tube in the case of *Xenopsylla* and the tracheal mouth in the case of *Bibio*.

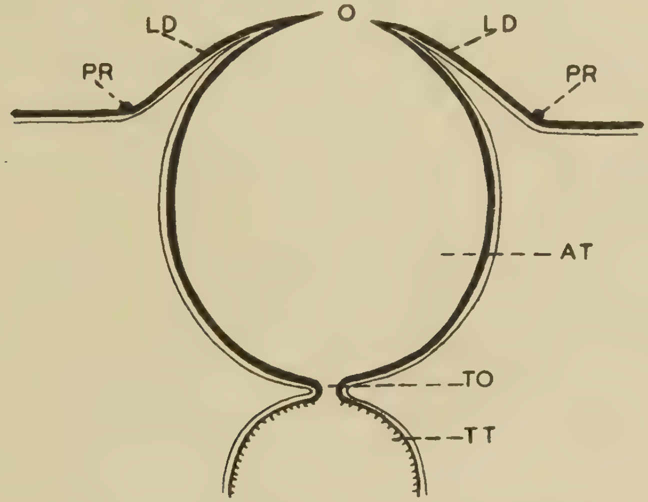
TIPULIDAE.

Tipula sp.

The Thoracic Spiracles.

The anterior thoracic spiracle (pl. VI, figs. 1 and 2) lies in a yellow membranous area between the bases of the first and second legs with its dorsal end directed anteriorly. The outer border of the spiracular lids (LD) is marked by a thin peritreme (PR), extending in a triangular plate (pl. VI, fig. 1 : PT) at the dorsal end of the spiracle. Internally this plate is continuous with the antero-dorsal wall of a dilated sac or vestibule (pl. VI, figs. 1 and 2 : V), which, after passing inwards, opens into the trachea by a large, oval fissure (pl. VI, figs. 1 and 2 : O, also *vide* text-fig. 8, which is a schematic longitudinal section). A few clusters of short hairs (pl. VI, fig. 1 : H) arise on the lids, but none of these project over the opening. A long, fan-like muscle (pl. VI, figs. 1 and 2 : CM) is inserted partly on to the ventral edge of the lids where they fuse together, and partly on the internal surface of the peritreme. If the insect is forced to struggle, the spiracular lids open and close rhythmically. Opening begins at the ventral end and progressively extends upwards until it reaches the dorsal end of the lids. The closing wave starts from the dorsal end and moves down along the lids. When the latter meet, their inner edges incline slightly inwards and the postero-dorsal lid overlaps the edge of the antero-ventral.

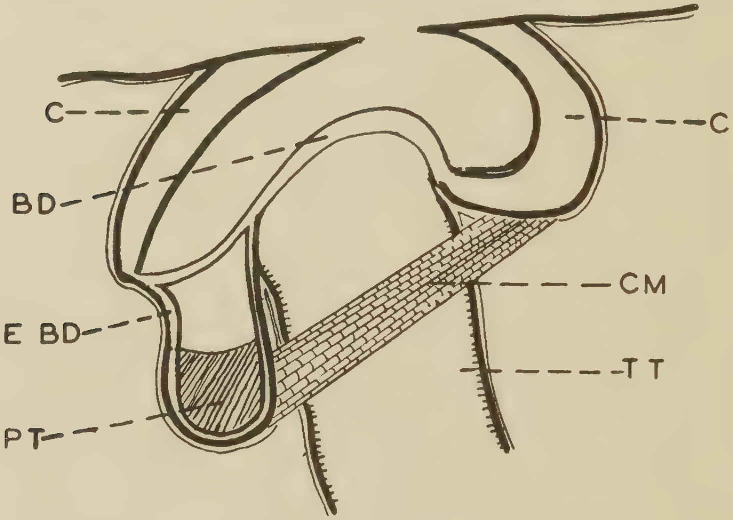
The second, or metathoracic spiracle (pl. VI, figs. 3 and 4), is more complex than the first. From the outside it is seen as a slightly oblique vertical slit enclosed by two thin transparent valve-like lids (LD), which protrude above the surface of the body and appear to be situated on the limb base of the third leg, extending beneath the haltere. Around the anterior and ventral margins of the lids, the integument is elevated and forms a sclerotic plate or a peritreme. This seems to protect the protruding lids, which, like the peritreme, show a marked constriction in the middle. At this place, a membranous fold (pl. VI, fig. 3 : F) arises from the wall of the posterior lid and extends obliquely to the opposite side where it continues in a groove in the anterior lid. The spiracular cavity is, therefore, divided into two : a small dorsal chamber leading to a large ventral one. The latter is continuous with a greatly dilated vestibule opening into the tracheae. Externally the vestibule is bounded by the above-mentioned fold and internally by the tracheal opening. A large sclerotised plate extends inwards from the pleura and curves over the anterior wall of the vestibule and the tracheal tube, forming a protective shield. Arising from the inner wall of the ventral part of each lid, just behind the external opening, are a few cuticular processes which fuse together to form two bands. The latter unite at the base to form a weak calliper (pl. VI, fig. 4 : CR). A fan-like closing muscle (pl. VI, figs. 3 and 4 : CM), which originates from the pleural wall (pl. VI, fig. 3 : PL) above the limb base of the third leg, is inserted on the basal connection of the calliper. On muscle contraction, the two sides of the ventral part of the lids are brought together, closing the opening to the tracheae. As soon as the muscle relaxes, the lids regain their previous position and leave the opening free. From anatomical considerations, as well as from observations on the living or anaesthetised insects, it appears that in this case the regulatory mechanism is not an efficient one. It can be seen from pl. VI, figs. 3 and 4, that the calliper and the closing muscle are small in proportion to the size of the lids.



Text-fig. 8.—Schematic longitudinal section of a thoracic spiracle of *Tipula* sp.

The Abdominal Spiracles (pl. VI, figs. 5A and 5B).

The abdominal spiracles are seen through the body wall, owing to the dark colour of the regulatory apparatus, as small black spots placed in the middle of the pleura. Normally, they are covered by the tergal plates, which overlap the pleura. In females, however, at the climax of egg development, the spiracles are exposed, and under these conditions they are always found open. The simple spiracular opening possesses no peritreme, and is partly surrounded by a few short unbranched hairs. Directly behind the external opening is a darkly pigmented collar (pl. VI, figs. 5A and 5B : C) attached at its broad end and mostly on the inner surface of the pleura but also to the mouth of the tracheal tube in a region devoid of taenidia (*vide* text-fig. 9, which is a schematic longitudinal section of an abdominal spiracle). The two arms of the collar differ in their structure and function. One is longer, more darkly pigmented, and more rigid than the other, extending down and alongside the tracheal mouth and supplying a rigid base for closure. The other is shorter and broader, and is situated nearer the external opening, where it is mostly attached to the inner surface of the pleural wall. Its free end is thrown into flexible ridges or bands (pl. VI, figs. 5A and 5B : BD), which are almost opposite the rigid arm and in direct connection with a semi-lunar plate (PT). The latter is placed on one side of the tracheal tube at the beginning of the spiral thickenings. Its border is darker in colour and more rigid than the flexible middle section. The side of the plate opposite the cuticular ridges articulates with the distal part of the rigid arm of the collar by means of elastic bands (EBD), which counteract the force exerted by the muscle during contraction. The closing muscle (CM) is rather broad and lies obliquely alongside the beginning of the tracheal tube between the two extremities of the regulatory apparatus, that is, between the base of the broad arm and that of the semi-lunar plate. The collar is attached to the pleural wall in such a way as to leave the ends of its arms hanging freely inside the body cavity (as shown in text-fig. 7), supported only by the surrounding tissues and the musculature of the body wall. When the muscle contracts, it draws the broad arm of the collar down a little and towards the opposite arm. In so doing, the plate moves upwards along the surface of the tracheal tube. This is possible owing to the elastic nature of the bands, which extend



TEXT-FIG. 9.—Schematic longitudinal section of an abdominal spiracle of *Tipula* sp.

to facilitate its movement. As a result of the movements of the broad arm of the collar and of the plate, the above-mentioned ridges are pressed against the longer arm of the collar, thus squeezing the tracheal entrance between them and occluding its opening. As soon as the muscle relaxes, the elastic bands " recoil " and draw the plate back to its previous position. This results in the separation of the ridges from the opposite arm of the collar and the tracheal opening is left free.

Rhyphidae.

Anisopus fenestralis (Scop.).

The Thoracic Spiracles (pl. VII, fig. 1).

The anterior thoracic spiracle is oval in shape and lies, with its narrower end inclined forwards, in a triangular area between the base of the first leg and the tergal plate. The spiracular opening (O) is a simple long fissure bordered on either side by the lids (LD) which are demarcated from the rest of the pleura by a thin peritreme (PR) interrupted near its ventral end. On the lids and projecting over the opening are short fine hairs (H). The closing muscle (CM) is rather strong and composed of about six bundles, each consisting of a large number of fibres. Its broad base arises on an apodemal ridge (RD), while its other end is inserted on the base of the spiracular lids at their point of fusion. On contraction, the closing muscle draws the lids inwards until the spiracle is closed.

The posterior thoracic spiracle (pl. VII, fig. 2) lies in a membranous area between the second and third limb bases and the root of the haltere, with its longitudinal axis inclined backwards. The spiracular lids (LD) are long, narrow, soft regions of the pleural wall. Their inner edges are thickened to form a ring (R) bordering the narrow spiracular opening (O). The peritreme and the lids are covered with fine hairs (H). Contraction of the muscle brings the two lids together until the sides of the ring meet and close the fissure. Because of the elasticity of the ring and the lids, they separate as soon as the muscle relaxes and leave the opening free.

The Abdominal Spiracles (pl. VII, figs. 3, 4A and 4B).

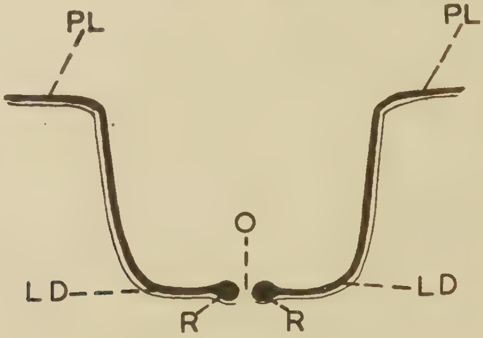
These lie on the upper edges of the pleural plates protected by long unbranched hairs arising from a thin oval peritreme and from irregular darkly pigmented rings around the distal part of the atrium (AT). The wall of the latter is for the most part membranous, only its proximal end, near the inner atrial opening, is sclerotised and forms a firm base for closure (the bridge : pl. VII, figs. 3 and 4B : B). On either side of the atrial wall, there is a sclerotised band (pl. VII, figs. 3 and 4A : BD) extending inwards from the above-mentioned rings and continuous with a lever (pl. VII, figs. 3, 4A and 4B : L) which lies to one side of the entrance to the trachea. In the open condition (pl. VII, fig. 3), the lever lies alongside the beginning of the atrial tube. On muscle contraction, the free end of the lever is pulled upwards (*vide* pl. VII, figs. 4A and 4B) towards the atrial wall. The lever's head, together with the band, are accordingly pushed inwards against the bridge and close the inner atrial opening (as shown in pl. VII, fig. 4B) which is situated just above the tracheal mouth. As the muscle relaxes, the elasticity of the band and the atrial wall causes tracheal opening.

SIMULIIDAE.

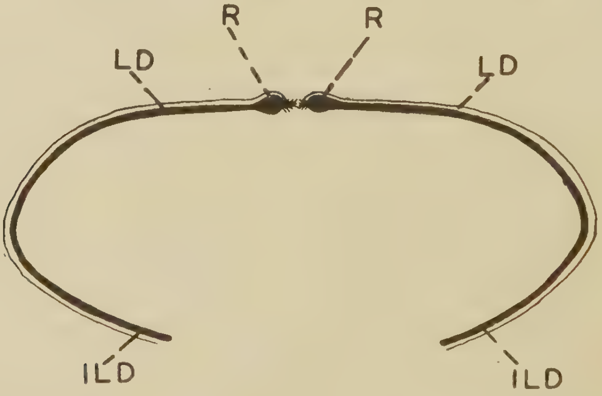
Simulium sp.

The Thoracic Spiracles.

The anterior thoracic spiracle (pl. VIII, fig. 1) lies in a depression on the upper edge of the pleura of the first thoracic segment (as shown in text-fig. 10). The oval opening (O) is surrounded by rows of short hairs (H), some of which are longer and project over its ventral part. On either side of the opening is a spiracular lid formed from the thin transparent pleuron. The inner border of the lids is strengthened by an elastic ring (R). Ventrally the latter gradually passes into the basal connection of the lids. The closing muscle (CM) is rather long and fan-like. Its broad end has its origin on an apodemal plate (APT), while its narrow end is inserted on the ventral edge of the ring. The movement of the lids, as seen under the binocular microscope, seems to be very different from that found in other Diptera possessing the lid type of regulatory apparatus. When the muscle contracts the lids extend downwards and inwards until the edges of the ring (H) meet, thus closing the aperture between them. On muscle relaxation, the lids separate again by a complete reversal of these movements, thus opening the spiracle.



TEXT-FIG. 10.—Schematic section of anterior thoracic spiracle of *Simulium* sp.



TEXT-FIG. 11.—Schematic section of posterior thoracic spiracle of *Simulium* sp.

The second or posterior thoracic spiracle (pl. VIII, fig. 2) is represented by a long fissure (O), lying beneath the haltere. On both sides of the opening are two well-marked lids (LD), which project from the body wall and curve towards one another. These lids continue inside the body and there also incline towards one another, thus forming a flattened sphere open at the poles (text-fig. 11). The stigmatic opening is covered with short fine hairs (H) which arise from an elastic ring (R) at the inner border of the lids and possibly serve to filter off dust and other foreign substances which may otherwise enter the tracheal system and impair its efficiency. The short closing muscle (CM) is inserted on the elastic basal connection of the lids. The regulatory mechanism is different from that of the anterior thoracic spiracle described above. On muscle contraction, the lids move upwards and inwards towards the middle of the opening, until their edges meet. As soon as the muscle relaxes, they separate by sliding downwards and outwards towards the body surface.

The Abdominal Spiracles (pl. VIII, figs. 3A, 3B and 4).

The abdominal spiracles are small, round, or slightly oval openings (pl. VIII, figs. 3A and 3B : O) situated in the middle of the pleura. The spiracular opening is surrounded by a thin peritreme (PR) which is inflected inwards, and merges into a somewhat globular atrium (AT). From the peritreme arise a few hairs (pl. VIII, fig. 4 : H) directed towards the centre of the opening and extending for a short distance inside the atrium. At the narrow proximal end of the latter (pl. VIII, figs. 3A and 3B : AT) lies a small tracheal opening (pl. VIII, fig. 3A : TO) which is guarded on one side by an elastic band (pl. VIII, figs. 3A, 3B and 4 : BD) flexibly articulated with a comparatively large strong lever (L) lying close to the tracheal entrance, and on the other side by a sclerotised bridge (B) against which the band is pressed during closure. The closing muscle (CM) consists of a few more or less parallel bundles of fibres. It connects the free end of the lever with the atrial wall to which it is attached near the external opening. The mechanism of regulation is essentially the same as described in RHYPHIDAE (p. 125).

CULICIDAE.

The only available work on the spiracular regulatory apparatus of the CULICIDAE appears to be that of Alessandrini and Missiroli (1926), who investigated an unnamed species of *Anopheles*. The present work, of which an account follows, was carried out on *Anopheles maculipennis* and *Theobaldia annulata*.

Anopheles maculipennis Mg.

The Thoracic Spiracles.

In their investigation of the spiracles of *Anopheles* sp., Alessandrini and Missiroli described two on the thorax, one on either side, beneath the haltere. Each of these spiracles is a long narrow slit surrounded by a thick peritreme bearing numerous rigid hairs directed towards the opening. These two authors maintain that the trachea starts directly from the post-spiracular chamber without any " closing mechanism." From their description and figure (reproduced on pl. IX, fig. 3) it appears that they overlooked the anterior thoracic spiracle and also failed to recognise the regulatory apparatus of the posterior thoracic spiracle.

The anterior thoracic spiracle (pl. IX, fig. 1) of *A. maculipennis* lies obliquely under the tergo-pleural suture with its dorsal end directed posteriorly. The oval opening is bordered by a thickened, pigmented peritremal sclerite (PR), interrupted for a short distance both dorsally and ventrally, so as to form a band on either side of the lids. A few rows of hairs, arising from these bands, project over the opening. The narrow spiracular lids (LD) extend from the inner margin of the peritreme and cover the tracheal entrance; their free edges are strengthened by a feebly developed calliper (CR). The long, fan-like, closing muscle (CM) has its origin on an apodemal ridge (RD) and its insertion on the ventral end of the calliper. When the stigma is open, the lids lie close to the peritremal bands which, in this position, are slightly elevated above the surrounding body wall. During closure, the muscle pulls on the hinge of the calliper and forces its two sides to approach each other. In the process of opening and closing of the spiracle, the peritremal bands, together with the soft neighbouring pleura, show a movement corresponding to that of the calliper and the lids. When the muscle relaxes, the calliper and lids regain their former position by virtue of their own elasticity and that of the surrounding body wall, thus opening the spiracle.

The posterior thoracic spiracle (pl. IX, fig. 2) lies beneath the haltere and is covered with hairs which are both shorter and fewer in number than those of the anterior thoracic spiracle. The spiracular opening is a somewhat elongated slit, protected by two elevated lids (LD), the outer margins of which are thickened to form a peritreme (PR), while their inner margins are supported by a pigmented ring (R) to which the closing muscle (CM) is attached, after passing through the ventral edge of the peritreme. The closing muscle is broader and much shorter than that of the anterior thoracic spiracle and has its origin on an apodemal ridge (RD).

The regulatory apparatus is similar to that described above for the anterior spiracle, except that the calliper of the anterior spiracle is replaced by a complete ring. The mechanism involved in regulating the size of the spiracular opening is the same in both cases.

The Abdominal Spiracles (pl. IX, figs. 4, 5 and pl. X, figs. 1, A, B, C, D and E).

Alessandrini and Missiroli (1926) gave the following general description of the abdominal spiracles of *Anopheles* sp. The elliptical spiracular opening is surrounded by a peritreme from which arise numerous rigid hairs directed towards the opening and acting as a filter. The post-spiracular chamber is divided into two very distinct sections: an anterior slightly conical section from which arise a few rigid hairs directed towards the lumen, and a posterior dilated region. The latter is a sac-like structure lying to one side of the atrial chamber and containing a mobile chitinous body (likened by the authors to a swallow's nest). By the contraction of bundles of muscle fibres, the latter is drawn up against a chitinous membrane which, situated opposite to it and between the two divisions of the atrium, functions like a cover or valve. Hence the outer and the inner sections of the atrium are disconnected. That closure is not hermetic is shown by the fact that *Anopheles* is easily affected by certain toxic gases. In illustration of these conclusions, the authors gave three figures (reproduced in pl. IX, figs. 6A, 6B and 6C).

My own observations on *Anopheles maculipennis*, however, have failed to confirm Alessandrini and Missiroli's descriptions of the structure of the abdominal spiracles. The spiracular opening leads into a well-defined atrium guarded by irregular sclerotic rings (pl. IX, figs. 4, 5 and pl. X, figs. 1B, 1C, 1D and 1E : R). In the open condition the atrium consists of a narrow outer section (pl. IX, fig. 4 : AT_1), guarded by a few long hairs (H), which opens into a dilated chamber (AT_2). On one side of this chamber is situated a large lever (pl. IX, figs. 4 and 5 : L), the head of which is flexibly articulated with a band (BD) attached to the atrial wall. At the narrow tracheal entrance there is a knob-like process (pl. IX, fig. 5 : pl. X, fig. 1D : K) projecting (when the apparatus is closed) into the narrow proximal end of the atrium and providing a firm base for closure. The closing muscle (pl. IX, figs. 4, 5 : pl. X, figs. 1B, 1C, 1D and 1E : CM) is attached along the free end of the lever and to the atrial wall opposite the lever's head. The mechanical factors involved in regulating the size of the tracheal opening are the same as described above in the case of Mecoptera (pp. 111, 112). As in the latter, the two points of muscle attachment are those best suited for producing a rotary motion together with a translatory one. On contraction of the muscle, these result in movement of the lever and the band downwards (towards and alongside the tracheal mouth), and inwards, whereby the band comes against the knob-like process. Meanwhile, the atrial wall follows the movement of the band and thus extends in the same direction. Hence it appears in the closed condition more elongated and closer to the lever (as shown in plate IX, fig. 5). On relaxation of the muscle, the parts of the apparatus, owing to their elasticity and to that of the atrial wall, revert to their previous positions and again expose the tracheal mouth.

From the above description and figures it would appear, therefore, that *A. maculipennis* possesses an abdominal regulatory apparatus very different from that described by Alessandrini and Missiroli (1926). Their account is inaccurate in that firstly, they claimed that the apparatus is situated inside the atrial tube as a movable " chitinous " body, and secondly because their description and figures imply that the closing muscle lies across the atrial lumen and is attached to two points on its inner wall. The sclerotised parts of the regulatory apparatus, such as the levers and plates, are always situated external to the atrial or the tracheal lumen. The closing muscle cannot, for anatomical reasons, lie within the atrial or tracheal cavity. The inaccuracies of this account probably arise from a rather superficial examination of the spiracles and associated structures; had these authors observed the apparatus in the open condition they could hardly have failed to arrive at a correct interpretation of its structure and mechanism. Their figures (pl. IX, figs. 6A, 6B and 6C) do not, as they claimed, represent the apparatus in the open, half closed and closed condition, but in each case the tracheal passage is depicted as closed. As Janet (1902) has pointed out, the slightest pressure of the coverslip on the preparation produces a considerable deformation of the parts of the regulatory apparatus, which are, moreover, subject to displacement during preparation. Such disarrangement may well account for the slight differences in the figures of Alessandrini and Missiroli.

In the absence of other experimental evidence the susceptibility of *Anopheles* to certain toxic gases cannot be taken as proof that the closure of the spiracles is not hermetic, as Alessandrini and Missiroli infer. Regarded from an anatomical point of view only, the closing mechanism appears perfectly efficient.

Theobaldia annulata (Schrank).

Except in minor structural details, the anterior and posterior pairs of thoracic spiracles of *T. annulata* resemble those of *A. maculipennis* described above. The structure of the regulatory apparatus and the mechanism of regulation is also similar.

The abdominal spiracles (pl. X, figs. 2 and 3) are much smaller than those of *A. maculipennis*. The lever (L) is accordingly shorter. The closing muscle

(CM) is attached, as in the case of *Anopheles*, to the free end of the lever and to the atrial wall. Other morphological characters of the spiracles and the regulatory apparatus as well as the mechanism of regulation are as described above for *Anopheles*.

Brachycera.

BOMBYLIIDAE.

Bombylius major L.

The Thoracic Spiracles.

The anterior thoracic spiracle (pl. XI, figs. 1 and 2) is oval in shape and is situated in a membranous pleural area bounded dorsally by the tergo-pleural suture. The inner margins of the large stigmatic opening are deeply pigmented. The posterior margin is densely covered with short thick hairs, while from the anterior one arise long tapering hairs (H) directed backwards so as to cover the opening. From the stigmatic margins extend a wide vestibule (pl. XI, fig. 2 : V) with a mottled membranous wall, which opens into the tracheae. The distal part of this vestibule is strengthened with yellow cuticular elements and is supported on either side by a sclerotised plate. These two plates together form a calliper (CR). A strong fan-like closing muscle (CM) has its wide base on an apodemal plate (PT) while its narrow end is inserted on the ventral part of the vestibule between the bases of the calliper and the two stigmatic margins. Investigation of the regulatory mechanism in the living insects presented some difficulties on account of the numerous hairs covering the body. The manner of insertion of the closing muscle suggests that during closure the two opposite sides of the vestibule, where the calliper lies, move against each other and so close the opening between them. This mechanism was tested during dissection by a slight pressure or downward pull on the closing muscle and it was found that the distal part of the vestibule is squeezed between the two arms of the calliper. At the same time the opposite margins of the spiracle, owing to their close association with the calliper, moved feebly in the same direction. Conversely, on a gradual release of pressure the elasticity of the atrial wall caused a reversal in the direction of movement of the calliper.

The posterior thoracic spiracle (pl. XI, fig. 3) is oval in shape and lies beneath the haltere in a membranous area which partly protrudes over the spiracular margins. The latter are similar to those described above for the anterior thoracic spiracle. The two opposite walls of the wide vestibule (V), which extends inwards from the spiracular margins, are each supported ventrally by a strongly sclerotised bar (BA). The area between the latter and the spiracular margin is bridged by yellow cuticule. The closing muscle (CM), which is very similar to that of the anterior thoracic spiracle, is inserted on that portion of the vestibule which connects the bars with the margins. The regulatory mechanism is similar to that described above for the anterior thoracic spiracle.

The Abdominal Spiracles (pl. XI, fig. 4).

The abdominal spiracles are large openings placed on the upper edges of the pleura and are covered with long fine hairs (H) directed toward the middle of the spiracular opening. The latter leads to a narrow atrial chamber (AT) surrounded at its innermost end by a sclerotised collar (C). On one side, the collar broadens and is prolonged into a manubrium (N) which is connected with a three-armed plate (PT) by means of an elastic connection (E). This plate is highly sclerotised, one surface serves as an attachment for the closing muscle

(CM), while on the inner side is attached an elastic band (EBD) which lies to one side of the tracheal mouth. The long closing muscle (CM) is composed of three more or less parallel bundles of fibres, and is attached at its other end to the margin of the collar opposite to the plate. The broad side of the collar opposite the elastic band provides a firm base for closure. On contraction of the muscle, the elastic band is brought against the opposite side of the collar, thus closing the trachea, which becomes compressed between the two. The stresses set up in the deformed elastic connection or plate, and in the elastic band, cause the return of the various parts of the apparatus to their original positions as soon as the closing muscle is relaxed.

ASILIDAE.

Leptogaster cylindrica (Deg.).

The Thoracic Spiracles.

The anterior thoracic spiracle (pl. XII, figs. 1 and 2) is kidney-shaped and is situated at the anterior part of the prothorax, with its longitudinal axis at right angles to that of the body wall. The spiracular area surrounding the opening is in the shape of a triangle, the base of which is marked by the tergo-pleural suture. The opening (pl. XII, fig. 1 : O) of the spiracle appears as a depression in this area which is swollen above the level of the body wall. Along the anterior edge of the thick brown peritreme (PR) are long stiff yellow hairs (H) directed backwards and covering the opening. From the inner surface of the peritremal sclerite extend two membranous flaps (pl. XII, fig. 2 : MF) strengthened near their inner edges by a strongly sclerotised calliper (CR). A dilated vestibule is situated directly behind the calliper, the two arms of which are basally connected by a V-shaped elastic plate (E). The latter serves as an insertion of a strong fan-like closing muscle (CM) having its origin on the pleuron just above the first limb base. On muscle contraction, the elastic plate pulls the two arms of the calliper together. These in turn draw the flaps over the atrial opening, thus closing it. Reopening is mainly brought about by the elasticity of the basal connection of the calliper.

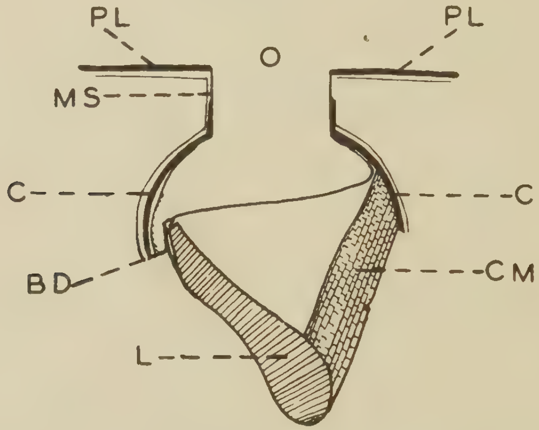
The posterior thoracic spiracle (pl. XII, figs. 3 and 4) is about half the size of the anterior spiracle and lies beneath the haltere with its narrow dorsal end directed backwards. The thick peritremal sclerite (pl. XII, fig. 3 : PR) encloses an elongated narrow opening covered with fine hairs (H) which arise from its anterior border.

The regulatory apparatus (pl. XII, fig. 4) consists of the same parts as those described above in the anterior thoracic spiracle. The calliper, however, shows some difference in its structure—the arms are much thinner while their bases are longer and more sclerotised than those of the anterior thoracic spiracle. The fan-shaped muscle (CM) takes its origin from an apodemal arm or ridge (RD) and is inserted on the basal connection (E) of the calliper which is here in the form of an elastic membrane.

The regulatory mechanism agrees in detail with that of the anterior thoracic spiracle.

The Abominal Spiracles (pl. XII, fig. 5).

These are situated on the upper halves of the pleura and lack peritremes. The simple opening (O) which is covered with rows of hairs arising from the body wall, leads directly to the tracheae, after the intervention of a narrow membranous strip (MS). From the inner surface of the pleura, arises a sclerotic collar (C) which may be likened to an inverted cup. Its distal narrow end is continuous with the membranous strip and embraces the beginning of the tracheal tube, while its proximal part extends down along the sides of the latter. The tracheal opening (TO) is guarded from one side by an elastic semilunar band (BD) continuous with the head of a lever (L). The latter is strongly sclerotised and lies to the side of the tracheal opening. Its free end serves as an attachment for a rather strong closing muscle (CM) which has its origin on the curved inner surface of the collar. The mechanism of regulation here is simple, but nevertheless efficient. Movement of the lever, on muscle contraction, results in the rotation of the lever's head in the opposite direction, so pressing the band against the opposite half of the tracheal mouth. In this position the closed tracheal mouth comes to lie against the curvature of the collar (as seen in text-fig. 12), which provides a firm base for closure. Owing to the elastic nature of the semi-lunar band, the spiracular and tracheal openings come into direct communication as soon as the closing muscle ceases to act.



Text-fig. 12.—Schematic section of abdominal spiracle of *Leptogaster cylindrica.*

Dolichopodidae.

Dolichopus festivus (Hal.) and *Dolichopus griseipennis* Stann were examined. The structure and mechanism of the regulatory apparatus in both species were found to be the same. The following is a description of *D. festivus* (Haliday).

Dolichopus festivus (Haliday).

The Thoracic Spiracles.

The anterior thoracic spiracle (pl. XIII, fig. 1) is a long fissure, lying above the first limb base and under the tergo-pleural suture. The spiracular opening (O) is bordered by a deeply pigmented peritreme (PR), which is discontinuous at the posterior edge of the spiracle. From the anterior border of the latter arise long hairs (H) directed backwards over the spiracular opening, the posterior margin being covered with short thick hairs which project in all directions. Directly beneath the external opening are a few elastic sclerotised rings (*vide* pl. XIII, fig. 2 : R) placed at the distal end of a very narrow vestibule. Attached to the ventral edge of these rings is a long, slender closing muscle (CM) consisting of three or four small bundles, each composed of relatively few fibres. It arises on an apodemal ridge (RD) just above the limb base of the first leg. Contraction of the muscle brings the two opposite sides of the rings together. These compress the distal part of the vestibular wall and thus close the orifice leading to the tracheae.

The posterior thoracic spiracle (pl. XIII, fig. 2) is a more or less circular opening (O) which lies in a depression beneath the haltere and above the third limb base. From the anterior margin of the spiracle arise some very long tapering hairs (H), which are directed backwards so as to cover the spiracular opening. A few elastic sclerotised rings (R), like those of the anterior spiracle, surround the distal part of a narrow vestibule. The closing muscle (CM) is stout and is composed of about seven bundles of fibres. Its broad base arises on an apodemal ridge (RD) above the third limb base, while its narrow end is inserted on the base of the rings.

The regulatory apparatus resembles that of the anterior thoracic spiracle in its structure and mechanism.

The Abdominal Spiracles (pl. XIII, figs. 3 and 3A).

The abdominal spiracles lie in the middle of whitish membranous pleura. The circular or oval spiracular opening (pl. XIII, fig. 3A : O) is bordered by a few hairs (H) arising from the neighbouring body wall. A few spiral thickenings, slightly thicker than individual taenidia, start from the stigmatic opening and are surrounded after a short distance by a broad deeply pigmented collar (pl. XIII, figs. 3 and 3A : C). The latter is produced at its broadest part into a manubrium (M) which is, however, less prominent than that in BOMBYLIIDAE. A strong lever (L), the head of which is flexibly articulated with the main part, is situated at the tracheal mouth near the manubrium. The head of the lever is connected on one side to the collar by means of an elastic semicircular band (BD) surrounding one-half of the tracheal tube (TT), while on the other side it joins the taenidia bordering the tracheal entrance. The closing muscle is strong and consists of a few bundles of fibres which run parallel to each other. This muscle is attached to one side of the lever and to the inner rim of the collar opposite the lever's head and the manubrium. Contraction of the muscle pulls the lever upwards and its head inwards (*vide* pl. XIII, fig. 3A), so that the head of the lever is brought against the manubrium.

EMPIDAE.

Empis livida L.

The Thoracic Spiracles.

The anterior thoracic spiracle (pl. XIV, fig. 1) is oval and lies in a sclerotic pleural area above the first limb base. Arising from the peritreme (PR) are finely branched yellow hairs similar to those found on the posterior thoracic spiracle (pl. XIV, fig. 2). These constitute an efficient filter for the spiracular opening. Directly beneath this filter are situated two membranous flaps (MF), the thickened inner margins of which form an elastic ring (R). The peritremal sclerite extends farther inwards towards the ventral part of the spiracle so as to form a ridge (RD) which supports a small fan-shaped closing muscle (CM), the narrow end of which is inserted on the base of the ring. The spiral thickenings marking the beginning of the tracheae start directly from the outer margin of the flaps. On muscle contraction, the ring draws the flaps inwards, thus closing the tracheal mouth. On relaxation of the muscle, the ring and flaps revert to their original positions by virtue of their elasticity.

The posterior thoracic spiracle (pl. XIV, fig. 2) lies beneath the haltere. It is covered with long branched hairs which arise on either side of a longish oval peritreme (PR) and form an efficient filter apparatus (FA). Two membranous flaps, similar to those of the anterior spiracle, are situated at the tracheal entrance, and are supported at their inner rims by a ring (R). The base of the latter passes through the peritremal sclerite which is here further inflected inside the body. The small fan-like closing muscle (CM), which arises from a rather broad pleural plate (PT), is inserted on the ventral end of the ring.

The regulatory apparatus and its mechanism is as described above for the anterior thoracic spiracle.

The Abdominal Spiracles (pl. XIV, fig. 3).

The abdominal spiracles lie in the middle of soft greyish pleura and are surrounded by long yellow hairs which are arranged to form a protective cone over the opening. To the inner surface of the pleural wall just behind the spiracular opening is attached a darkly pigmented collar (C), the two arms of which surround the tracheal mouth. Of the two arms, the thinner is situated closer to the external opening, while the broader arm extends alongside the tracheal entrance. The broader arm of the collar is articulated with the head of a large strong lever (L), by a few cuticular strands, and provides a firm base for the regulatory apparatus. The other side of the head of the lever is extended into an elastic band (BD), placed around one-half of the tracheal tube opposite the broader arm of the collar. The closing muscle (CM) is strong and is composed of five bundles, each consisting of a large number of fibres. This muscle is attached along one surface of the lever, and, after passing alongside the tracheal mouth, has its origin on the inner margin of the collar opposite to the head of the lever. On muscle contraction, the lever is pulled upwards and inwards in the direction of the force, with the result that the band is brought against the broader arm of the collar, thus compressing the tracheal mouth. As soon as the muscle relaxes, the lever drops to the side of the tracheal tube, and the band, owing to its elasticity, returns to its original position and leaves the tracheal mouth free. The movement of the band towards and away from the collar is facilitated by its flexible articulation with the lever.

Cyclorrhapha.

Aschiza.

SYRPHIDAE.

The thoracic regulatory apparatus of *Eristalis* was described by H. Landois (1867) under the name of "buzzing apparatus" (Brummapparate) since he thought it was responsible for the humming produced by the insect during flight. Gäbler (1930) appears to be the only author who has made any detailed investigation of the "closing apparatus" of the SYRPHIDAE in recent years. This worker has studied both the thoracic and abdominal spiracles of *Eristalis tenax* L. In the present work *Rhingia campestris* Mg., *Syrphus balteatus* (Deg.) and *Platychirus peltatus* (Meig.) have been investigated as representatives of the family SYRPHIDAE.

Rhingia campestris Mg.

The Thoracic Spiracles.

The anterior thoracic spiracle lies on the prothorax directly behind the head and above the first limb base. Structurally it is exactly like that of *Eristalis tenax* as described and figured by Gäbler (1930). The spiracular opening is regulated by two elastic membranous flaps, at the ventral ends of which the closing muscle is inserted on an elastic plate. In *Eristalis*, these flaps were called by Gäbler " closing lips " and he regarded them as simple folds of the tracheae. Contrary to Gäbler's statement, these structures are always devoid of taenidia, and are actually folds of the most distal parts of the membranous wall of the vestibule.

The structure and mechanism of the regulatory apparatus is essentially similar to that of *Eristalis* as described by Gäbler (1930).

The posterior thoracic spiracle (pl. XV, figs. 1A, 1B, 2A and 2B) is more complicated than the anterior thoracic. It is larger in size than the latter and lies below and slightly in front of the haltere. Its external structure is very much the same as Gäbler found in *Eristalis tenax*. Beneath the hairy cover of the spiracle, there are in *Rhingia* two membranous flaps (pl. XV, figs. 1A and 2A : MF), arising from the internal surface of the peritreme (pl. XV, fig. 1A : PR). Their inner rims are made up of a succession of sclerotic thickenings alternating with narrow elastic membranous areas, and supported with an elastic ring (R). Directly behind these flaps is a wide vestibule (pl. XV, fig. 1B : V), the distal part of which is continuous with the internal surface of the flaps and is thrown into thick lamellae (pl. XV, figs. 1A, 1B and 2B : IP) arranged alternately, two on each side. These lamellae, the structure of which is similar to that of the flaps, project into the cavity of the post-spiracular chamber. In *Eristalis*, according to Gäbler, the lamellae are simple folds of the tracheae and have about fifteen transparent lobes on either side. They were taken by Landois for " voice leaves," by the vibration of which the well-known sound of these insects is produced. From the internal surface of the outer margin of the flaps two heavily sclerotised bands (pl. XV, figs. 1A, 1B, 2A and 2B : BD) arise. These are continuous for the most part with the inwardly inflected peritreme, and support the flaps and the lamellae. The closing muscle (pl. XV, figs. 1A, 1B, 2A and 2B : CM) is rather stout and is composed of a large number of bundles of fibres. It is inserted on an elastic plate (pl. XV, fig. 2A : E) which is actually the combined base of the flaps and the lamellae together. The broad base of the closing muscle arises on an apodemal plate (pl. XV, figs. 1A and 1B : PT) which is an extension of a strongly sclerotised ridge surrounding the dorsal and the anterior part of the dilated post-spiracular chamber forming, with the bands, a protective arrangement for the latter. On muscle contraction, the flaps approach each other, causing the lamellae to lock together and so close the opening between them (pl. XV, fig. 1B). Gäbler maintains that as a result of muscle contraction in *Eristalis*, the two sides of the tracheae are brought together. It seems unlikely that this is the case as the muscle is inserted on the base of the flaps and that of the distal part of the greatly dilated vestibule (the lamellae), which is placed above the tracheal entrance. Hence muscle contraction cannot affect the trachea, which is situated farther inwards, its two sides remaining apart, whether the spiracle is open or closed.

Opening is mainly affected by the energy stored in the elastic plate connecting the base of the flaps and the lamellae and also in the sclerotic thickening at their inner rims. These thickenings " uncoil " when the muscle relaxes and restore the flaps and the lamellae to their original configuration, thus leaving the spiracular opening free.

The Abdominal Spiracles (pl. XVI, figs. 1A and 1B).

Gäbler gave incomplete descriptions of the abdominal spiracles of *Eristalis* and their " closing mechanisms." No muscles were mentioned or figured by him.

In *Rhingia campestris* the abdominal spiracles are situated at the upper edges of the pleura, and are surrounded by darkly pigmented, oval peritremes, from which arise branched hairs covering the spiracular openings. These hairs extend for a short distance inside the atrium (pl. XVI, fig. 1B : AT). The wall of the latter is sclerotic and narrows gradually as it proceeds inwards, becoming more elongated just above the tracheal mouth (TO). A part of the atrial wall is more thickened and forms a firm base for closure (the bridge) (pl. XVI, figs. 1A and 1B : B). A strong lever (L), which is flexibly articulated with the bridge (*vide* pl. XVI, fig. 1A), lies at the tracheal entrance. The head of the lever extends from one side in the form of an elastic semi-lunar band (pl. XVI, figs. 1A and 1B : BD) round one-half of the tracheal tube opposite the bridge. The closing muscle (CM) is composed of a number of more or less parallel bundles of fibres. It is attached to the surface of the lever and to the atrial wall near the narrow end of the bridge. In *Eristalis*, Gäbler only mentioned a closing cone (homologous with the lever), a closing bridge and a closing band. On contraction of the muscle, the free end of the lever is raised and its head is pushed inwards whereby the band comes against the bridge and closes the slit leading to the tracheae (*vide* pl. XVI, fig. 1B). Owing to the flexible articulation of the lever, and to the elastic nature of the band, both return to their positions as soon as the muscle relaxes, thus leaving the tracheal opening freely exposed.

Syrphus balteatus (Deg.).

Apart from minor structural differences, the thoracic spiracles (pl. XVI, fig. 2) and their regulatory apparatus are of the same general form as those of *Rhingia* described above. The supporting bands of the second thoracic spiracle are, however, less prominent.

The abdominal spiracles (pl. XVI, fig. 3) are placed at the upper edges of the pleura as are those of *R. campestris*. As in the latter, the spiracular opening is bordered by a peritreme from which arise long branched hairs covering the opening. The peritremal sclerite extends inwards along the atrial wall (AT) which becomes progressively narrower until it opens into the tracheae. At this narrow portion, between the atrium and the tracheae, a strong lever (L) is placed. Its head is produced into a band (BD) around one-half of the tracheal entrance, opposite a sclerotic part of the atrial wall which forms a bridge (B). The regulatory mechanism is similar to that described above in *R. campestris*.

Platychirus peltatus (Meig.).

The regulatory apparatus found on the thorax and on the abdomen agree with that of *Syrphus balteatus*. There are, however, slight differences in the size of the stigmata and in the hairy cover.

The regulatory mechanisms of both the thoracic and abdominal stigmata are the same as described above in *R. campestris*.

Cyclorrhapha.

Schizophora.

Acalypterae.

DROSOPHILIDAE.

Drosophila melanogaster (Auctorum).

The Thoracic Spiracles.

The anterior thoracic spiracle (pl. XVII, figs. 1, 2A and 2B) is oval in shape and placed above the anterior limb base with its longitudinal axis vertical to that of the body. It is protected by a cone formed from long hairs (pl. XVII, fig. 1 : H) which arise from a thin peritreme (PR). Beneath this hairy cover are two membranous flaps (pl. XVII, fig. 2A : MF) covering the tracheal entrance. Their inner rims are thickened to form an elastic ring (pl. XVII, figs. 2A and 2B : R), and, particularly near their bases, they are supported by cuticular elements and an elastic membrane forming a plate (E). The fan-like closing muscle (CM) has its broad base on a Y-shaped apodemal ridge (RD) and its narrow end on the elastic plate connecting the bases of the flaps. Muscle contraction brings the flaps together in the usual way.

The cuticular elements at the lower parts of the flaps clip the ventral portion of the ring during closure (as seen in pl. XVII, fig. 2B) and so add, by virtue of their elasticity, to the efficiency of the opening and closing of the spiracle.

The posterior thoracic spiracle is placed just above the third limb base with its longitudinal axis lying obliquely to that of the body. It is smaller and more round in shape than the anterior spiracle, but is otherwise identical in structure and mechanism with the anterior thoracic spiracle.

The Abdominal Spiracles (pl. XVII, figs. 3A, 3B, 4A and 4B).

These are very small openings (pl. XVII, figs. 3A and 3B : O) lying at the upper edges of the pleura, without any hairy cover, except for a few hairs arising from the neighbouring parts of the body wall. There is a well-developed atrium, the membranous walls of which (pl. XVII, figs. 3A, 3B, 4A and 4B : AT) are supported by spiral thickenings or irregular rings (R) continuous with the cuticle of the body wall. The end portions of these rings form two bands (pl. XVII, figs. 3A, 3B, 4A and 4B : BD) passing along the proximal part of the atrial wall and placed just above the very narrow tracheal entrance where they become more sclerotised to form parts of the regulatory apparatus. One of these bands passes by the head of a lever (pl. XVII, figs. 3A, 3B and 4B : L) and then joins the taenidia surrounding the tracheal mouth, whereas the other is produced at its tip into a knob-like process (pl. XVII, fig. 4B : K) situated at the tracheal orifice opposite the lever's head so as to provide a firm base for closure. Similarly the part of the atrial wall close to the knob is sclerotised and gives a further support to the head of the lever during closure. The latter is a short stick-like arm lying at the narrow proximal end of the atrium just at the beginning of the tracheal tube. The closing muscle (pl. XVII, figs. 3A, 3B and 4B : CM) consists of three or four slender bundles, each of which is composed of a small number of fibres. These bundles run more or less parallel to each other between the free end of the lever and the atrial wall where they are attached to the band near the lever's head. Contraction of the muscle pulls the free end of the lever upwards and causes an inward inclination of its head, which is thereby brought against the knob-like process and closes the tracheal mouth. The elastic nature of the bands and the proximal part of the atrium causes the tracheal mouth to be opened as soon as the muscle relaxes.

ORTALIDAE.

Platystoma seminationis (Fab.).

The Thoracic Spiracles.

The anterior thoracic spiracle (pl. XVIII, figs. 1, 2A and 2B) is oval and lies above the first limb base beneath the tergo-pleural suture, with its longitudinal axis vertical to that of the body wall. From the thick peritreme (pl. XVIII, fig. 1 : PR) arise very long tapering hairs which form an efficient cover to the spiracular opening. Attached to the internal surface of the peritreme are two membranous flaps (pl. XVIII, figs. 2A and 2B : MF), the bases of which are connected by an elastic plate (E). Structurally, the inner rims of the flaps are similar to those of the posterior thoracic spiracle of *Rhingia campestris* described above (p. 135). The strong closing muscle (CM) is fan-shaped and has its broad base on a thick ridge (RD) passing alongside the flaps, while its narrow end is inserted on the elastic plate. The mechanism of regulation is the same as in *Drosophila melanogaster*. Pl. XVIII, figs. 2A and 2B show the stigma in the open and closed condition.

The second thoracic spiracle (pl. XVIII, fig. 3) lies beneath and a little in front of the haltere. It is circular in shape and covered with long yellow hairs which arise from a thick peritreme surrounding the opening. Two membranous flaps (MF) arise from the internal surface of the peritremal sclerite and have the same general structure as those of the anterior thoracic spiracle. Situated between the flaps and the beginning of the tracheae is a greatly dilated vestibule which is much larger than that found in the anterior spiracle. Its walls are very soft and have a mottled (cellular) appearance. Nearly at the middle of this vestibule there is an oval sclerotised ring, the function of which is probably to keep the vestibular walls apart. From this ring a few short hairs project into the atrial lumen. The closing muscle (CM) is fan-shaped and composed of a large number of bundles of fibres. It arises on a ridge (RD) and is inserted on an elastic plate (E) connecting the flaps.

The structure and mechanism of regulation is as described above in the anterior thoracic spiracle.

It appears from the size of the flaps and the muscle that the mechanism of regulation is more efficient in the second than in the first thoracic spiracle.

The Abdominal Spiracles (pl. XVIII, fig. 4).

These are medium-sized circular openings covered with long hairs extending for a short distance inside the atrium. The latter is of a considerable size and is similar in its structure to that of *Drosophila* (see page 137).

Apart from minor structural differences, the regulatory apparatus agrees in its main features with that of *Drosophila*. The knob, however, is not apparent here and, during muscle contraction, the spurred head of the lever comes against the opposite band and the sclerotised part of the atrial wall close to it, thus closing the entrance leading to the tracheae. Opening takes place on muscle relaxation owing to elasticity of the bands and the proximal part of the atrial wall.

CORDYLURIDAE.

The two species *Scatophaga stercoraria* (L.) and *Scatophaga decipiens* (Hal.) were investigated, the former being examined in more detail.

Scatophaga stercoraria (L.).

The Thoracic Spiracles.

The anterior thoracic spiracle (pl. XIX, fig. 1) is oval and lies above the first limb base with its dorsal end directed slightly backwards. It is protected with a thick hairy cover arising from the peritremal sclerite, the hairs pointing towards the mid line of the spiracular opening. Two membranous flaps (MF) are situated directly under the hairy cover at the distal end of a wide vestibule leading to the tracheae. Their edges are supported by an elastic ring (R) which shows in some parts annular or spiral sclerotic thickenings alternating with the membranous parts of the flaps. The closing muscle (CM) is fan-like and originates on a U-shaped apodemal ridge (RD). It passes upwards towards the base of the flaps where it is inserted on an elastic plate (E). The mechanism of regulation is essentially the same as in the Acalypterae described above.

The posterior thoracic spiracle (pl. XIX, figs. 2 and 3) is more or less circular in shape and lies beneath the haltere. It is covered with very long tapering hairs (pl. XIX, fig. 2 : H) which form an efficient filter for the opening. There are also some short thick hairs covering the peritreme. Two oblong membranous flaps (pl. XIX, fig. 3 : MF) arise from the inner edges of the peritreme and cover a wide vestibule leading to the tracheae. These flaps have marked transverse sclerotic thickenings and their inner edges are folded to form an elastic ring (R). The fan-shaped closing muscle (CM) arises from an apodemal ridge (RD) and is inserted on the base of the flaps and the ring.

The structure and mechanism of the regulatory apparatus is similar to that of the anterior thoracic spiracle described above.

The Abdominal Spiracles (pl. XIX, figs, 4A and 4B).

These appear as small black spots on the upper edges of the pleura. The spiracular opening is surrounded with a pigmented peritreme which is inflected inwards and then becomes continuous with the irregular sclerotic spirals passing along the atrial wall. Some short hairs arise from the peritreme as well as from the atrial wall and guard the tracheal entrance. The atrium (AT) gradually narrows down as it proceeds from the external aperture until it opens into the tracheae. At this place, the atrial wall is surrounded by an elastic band (BD) passing by the head of a strong lever (L) which lies to one side of the tracheal mouth. This band is a continuation of the sclerotic spirals of the atrial wall. The strong closing muscle (CM) has its attachments on the free end of the lever and on the atrial wall near the lever's head. Contraction of the muscle pulls the free end of the lever upwards towards the atrium and imparts an inward tilt to its head (*vide* pl. XIX, fig. 4B). As a result, the band is constricted at the middle portion, thus closing the passage between the atrium and the tracheae. On relaxation of the muscle, the tension of the elastic band is reduced so that it forces the wall of the atrium apart.

Scatophaga decipiens (Hal.).

Investigation of the thoracic as well as the abdominal spiracles showed that, although there are differences in size and shape, the structure and mechanism of the regulatory apparatus is in complete agreement with that found in *S. stercoraria* (L.).

BORBORIDAE.

The two species *Sphaerocera subsultans* (L.) and *Leptocera ferruginata* (Stenh.) were examined, the former in more detail.

Sphaerocera subsultans (L.).

The Thoracic Spiracles.

The anterior thoracic spiracle is oval in shape and lies on the pleuron just above the first limb base. It is covered with fine hairs which arise from a thick darkly pigmented peritreme bordering the spiracular opening and which extends towards its mid line.

The structure and mechanism of the regulatory apparatus agrees with that of the posterior thoracic spiracle described below.

The posterior thoracic spiracle (pl. XIX, fig. 5) is more or less a circular opening lying beneath the haltere and surrounded by a thick pigmented peritreme (PR) from which arise long unbranched hairs (H) protecting the spiracular opening. Two narrow membranous flaps (MF) emerge from the inner margin of the peritreme, their rims being folded to form an elastic ring (R). A fan-shaped closing muscle (CM) arises on an apodemal ridge (RD) and is inserted on the ventral part of the ring. Closure is effected in the usual manner.

The Abdominal Spiracles.

These appear under the binocular microscope as small dark areas in the middle of whitish transparent pleura. The spiracular opening leads to an elongated atrium in which two divisions are visible. The first or distal portion is characterised by its tubular form and brown walls which are traversed by a heavily pigmented spiral. This opens into a transparent, slightly globular portion traversed by a thin irregular elastic ring. The latter thickens just before the tracheal mouth and forms an elastic band, similar to that described above in CORDYLURIDAE (*vide* pl. XIX, fig. 4B : BD), continuous with the head of the lever, which lies to one side of the tracheal entrance. The closing muscle connects the free end of the lever with the atrial wall near the lever's head.

The structure and mechanism of the regulatory apparatus is as described above and figured in the case of CORDYLURIDAE.

Leptocera ferruginata (Stenh.).

The thoracic as well as the abdominal spiracles possess the same type of regulatory apparatus as that found on the thorax and on the abdomen of *Sphaerocera subsultans* (L.) mentioned above.

Cyclorrhapha.

Schizophora.

Calypterae.

TACHINIDAE.

Calliphora erythrocephala (Mg.).

H. Landois (1867) described an elaborate apparatus on the thorax of *Calliphora vomitaria*, to which he attributed the production of sound. Later (1890–2) a more or less similar apparatus for closing the tracheal system on the thorax of *C. erythrocephala* was described by Lowne. The latter author also mentioned and figured the abdominal spiracles.

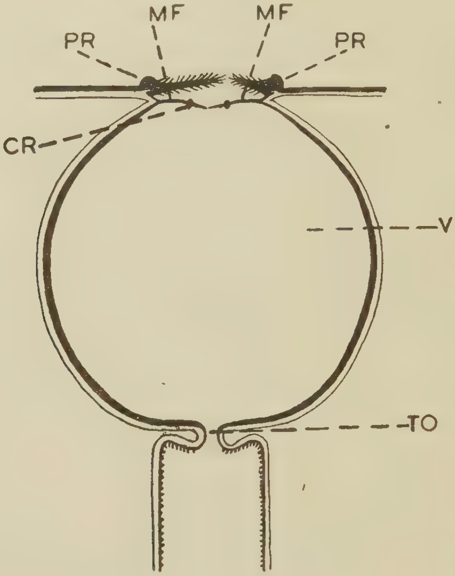
The Thoracic Spiracles (pl. XX, figs. 1, 2, 3 and 4).

According to Landois (1867), the " Brummapparate " or the sound apparatus of the anterior and of the posterior thoracic spiracles are similar, their main parts being: *A*. the buzzing cavity; *B*. the buzzing valve; *C*. the buzzing ring, and *D*. the distal part of the tracheae. He maintained that the anterior and posterior thoracic spiracles differ mainly in their external cover, the first being an oval fissure, the edges of which are protected with finely branched yellow hairs. The second he described as heart-shaped and covered with two unequal valve plates (buzzing valves), each of which is made up of stiff branching and interlacing hairs. The small valve is movably articulated and can be opened towards the outside. The larger valve, however, is fixed. Beneath these two valves lies the buzzing ring. This is oval and hangs freely in the buzzing cavity, except at its upper and lower poles where it is firmly attached to the surrounding buzzing cavity wall (atrial wall). Landois noticed that this ring was elastic and found that when dissected, the two sides fell apart owing to the presence of an elastic joint in the middle.

The present work on *C. erythrocephala* (Mg.) shows that the external morphology of the anterior and posterior thoracic spiracles is in complete agreement with that of *C. vomitaria*. The term " valve plates " for the hairy cover of the second thoracic spiracle, however, is misleading. Lowne (1900–2) had regarded them as consisting of thin membranes, strengthened by a number of dendriform tubes, and covered with numerous diverging hollow setae. While agreeing with Landois that the large valve plate is fixed, Lowne maintains that the outward movement of the small valve plate is due to dislocation. He states, however, that in *C. erythrocephala* the contraction of a small muscle attached to the fixed border of this valve plate causes its inward movement, thus opening the spiracle, and that air pressure in the vestibule causes its return to its original position. In this investigation it has been found that the outward and inward movements of this " valve " are due to its dislocation and not to muscular contraction or air pressure as Lowne supposed, since no muscles were found to be attached to its fixed border. The " closing apparatus " was thus wrongly described by Lowne as composed of an external and an internal valve—the former consisting of the two valve plates and the latter of a calliper-like sclerite and a small fan-shaped muscle.

In the course of the present investigation, the regulatory apparatus of the anterior and posterior (pl. XX, figs. 1, 2, 3 and 4) thoracic spiracles was found to be slightly different. The main parts are: (*a*) a ring (in the anterior thoracic) or a strongly sclerotised calliper (in the posterior spiracle), (*b*) two membranous flaps, (*c*) an elastic plate, and (*d*) a closing muscle. The flaps (pl. XX, fig. 3: MF) arise from the internal rims of the peritreme and extend over a greatly dilated vestibule situated above the tracheal entrance (*vide* text-fig. 13), being covered by long finely branching hairs which form an efficient filter to the spiracular opening. In the posterior thoracic spiracle, fine branches of these hairs come together and so form two separate divisions: a large and a small one. It was these that were termed " valve plates," though, as mentioned above, they are fixed and do not act as valves but function as a filter apparatus. On the inner rims of the flaps arises a ring (pl. XX, fig. 1: R) which is thrown in some parts into thin ridges alternating with narrow membranous areas of the flaps. The more sclerotised calliper (pl. XX, figs. 2, 3 and 4: CR) of the posterior thoracic spiracle is not found on the inner margin of the flaps, so that membranous parts of the flaps are left hanging into the vestibule. These were taken by Landois as " stimmbänder " or voice bands which rattled on passage of air in or out of the tracheae and produce the characteristic sound of these flies. The closing muscle (pl. XX, figs. 1, 2, 3 and 4: CM) consists of several bundles of fibres. It is longer and broader in the posterior thoracic spiracle than in the anterior one. Its broad base arises on a strong ridge (RD), while its narrow end is inserted on an elastic plate (pl. XX, figs. 1, 3 and 4 : E) at the lower end of the ring or connecting the two arms of the calliper together.

The mechanism of closure has been observed both by Landois and Lowne in the anterior thoracic spiracle after removal of the hairy cover. In this work, the mechanism of regulation in the posterior thoracic spiracle was investigated since it is larger and more easily manipulated than the anterior spiracle. If the hairy cover is removed the regulatory apparatus can be seen in action. During closure, the calliper draws the flaps upwards (in the plane of the body surface) and inwards (towards the middle of the opening) until the edges of the calliper touch each other and close the opening between them. The " voice bands " of Landois then hang downwards in the vestibule. The opening of the spiracle takes place, as soon as the muscle relaxes, by a reversal of this movement and the " voice bands " become inclined horizontally (as seen in pl. XX, fig. 3).



TEXT-FIG. 13.—Schematic section of thoracic spiracle of *Calliphora erythrocephala.*

The Abdominal Spiracles (pl. XXI, figs. 1, 2, 3A and 3B).

These are small circular openings encircled by peritremes from which arise inwardly directed hairs. The peritremal sclerite extends around the atrial wall in the form of rugose sclerotic rings, or spirals, and eventually merges into the regulatory apparatus. Some short hairs arise from the inner walls of the atrium and project into its lumen to prevent the intrusion of foreign substances. The atrium gradually narrows down until it opens into the tracheae. At this narrow portion the sclerotic rings become more irregular, and fuse together so as to form a strongly sclerotised triangular plate or bridge (B) surrounding one-half of the tracheal mouth. The opposite half, however, is marked by an elastic band (pl. XXI, figs. 2, 3A and 3B : EBD) stretched between the narrow end of the bridge and the lever (pl. XXI, figs. 2, 3A and 3B : L). The latter lies near the broad base of the bridge with which it is flexibly articulated. Some more or less parallel bundles of fibres forming the closing muscle (pl. XXI, figs. 2 and 3A : CM) are attached on the one hand to the atrial wall near the narrow part of the bridge, and on the other to the free end of the lever. Contraction of the muscle pulls the free end of the lever upwards so that its head is pushed inwards. The band is then pressed against the bridge, thus closing the tracheal entrance. The elasticity of the band tends to separate it from the bridge as soon as the muscle relaxes, thus leaving the tracheal opening free.

These conclusions differ considerably from those of Lowne (1900–2), whose account and figures are very erroneous and incomplete. Here also he described an external and an internal valve; the former situated at the inner extremity of the atrium and composed of a bow, a semi-lunar plate, a lever and a muscle; and the latter projecting into the tracheal trunk and separated from the external valve by a spiracular sac. As a result of this, Lowne's attempts to explain the mechanism of closure are incorrect.

ANTHOMYIIDAE.

The only previous work on the "closing apparatus" of ANTHOMYIIDAE seems to be that of Landois (1867), Landois and Thelen (1867) and Krancher (1881). *Musca domestica* L. is taken as a typical representative of this family. *Coenosia tigrina* (Fab.) was also investigated.

Musca domestica L.

The Thoracic Spiracles.

In his careful investigation of what he thought to be the " Brummapparate," Landois (1867) described what is actually the thoracic regulatory apparatus of *M. domestica.* Although Krancher (1881) agrees with Landois on the external morphology of the spiracles and the structure of the apparatus, he maintains, however, that its function is to close the spiracle, this being done by means of a fan-shaped closing muscle attached to the ring referred to by Landois as the " buzzing ring " (*vide* p. 141). Krancher's figures, therefore, owing to his better understanding of the structure and function of the apparatus, are more clear and correct than those given by Landois.

An account of the external morphology of the thoracic spiracles of *M. domestica* is to be found in the above-mentioned works of Landois and Krancher.

In the present investigation, the regulatory apparatus (pl. XX, fig. 5) of both the thoracic spiracles was found to be the same. It consists of the following parts : (*a*) two membranous flaps; (*b*) a ring; (*c*) an elastic plate, and (*d*) a closing muscle. A ring (R) borders the inner margin of two membranous flaps (MF), which are situated directly beneath the external opening, and are guarded by a thick hairy cover; a fan-like closing muscle (CM) originates on an apodemal ridge (RD) and has its narrow end on an elastic plate (E) at the lower edge of the ring and the flaps. This plate, on muscle contraction, draws the two sides of the ring together towards the mid line of the spiracular opening. Hence, the flaps stretch over the opening and cut off the air.

The Abdominal Spiracles (pl. XXI, fig. 4).

Investigating the " tracheal closing apparatus " in insects, Landois and Thelen (1867) found that in *Musca* (now *Calliphora*) *vomitoria* it consists of a strongly " chitinised " semi-lunar bridge connected from both sides by a thin band. At the place where the band joins the stronger part of the bridge, a stick-like lever is to be found. The free end of the latter is movable by means of a muscle, the contraction of which brings the band, as well as a triangular lid situated beneath it, against the bridge. These conclusions are supported by Krancher's work (1881) on *C. vomitoria* and *M. domestica.* This author maintains that in the latter the lever is considerably larger and that its free end is thickened to a knob. According to him, the closing hoop or bridge of *C. vomitoria* is reduced to a " chitin " strip.

The above-mentioned conclusions regarding *C. vomitoria* correspond to a considerable extent with the results recorded above for *C. erythrocephala.* It is most likely that the triangular plate mentioned by Landois and Thelen and referred to by Krancher is actually the bridge, which has a three-cornered appearance, especially when the apparatus is closed.

The abdominal regulatory apparatus of *M. domestica* (pl. XXI, fig. 4) was found to be a simple arrangement for pinching the proximal part of the atrium. It consists mainly of: (*a*) a lever; (*b*) a band, and (*c*) a closing muscle. The lever (L) is long and stick-like, with its head situated at the proximal part of the atrium, which is here very narrow, and surrounded by an elastic band continuous with the spiral thickening passing along the atrial wall. The free end of the lever is produced into a knob which is more prominent in the most anterior spiracles, and apparently gives an increased surface for the attachment of the closing muscle (CM). The other end of this muscle spreads out on either side of the lever and is inserted on the atrial wall. Krancher, however, described it as attached to the hypodermis of the body wall, but gave no figures to support this statement.

The mechanism of regulating the tracheal opening is simple but, nevertheless, very efficient. As the muscle contracts, the lever's head pushes one side of the elastic band, which lies in the region between the atrium and the tracheae, against the opposite side, thus cutting the communication between the two. As soon as the muscle relaxes, the lever goes back to its original position and leaves the tracheal entrance free.

Coenosia tigrina (Fab.).

No differences were found between the structure and mechanism of the regulatory apparatus of this species and that of *Musca domestica* L.

Cyclorrhapha.

Pupipara.

HIPPOBOSCIDAE.

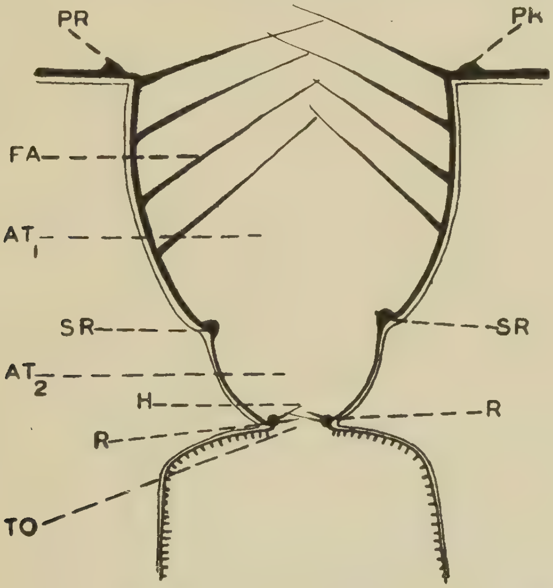
The previous work on the " closing apparatus " of Pupipara is that of Krancher (1881) and Alfonsus and Braun (1931). Investigating the " closing apparatus " of *Melophagus ovinus*, the first author claimed that although the thoracic and abdominal spiracles of this species differ morphologically, they possess the same type of " closing apparatus," and are distinguished only by the more powerful form of the thoracic spiracles. He did not describe or figure, however, the regulatory apparatus found on the thorax, and gave two incorrect figures (Nos. 6 and 7, pl. XXVIII) for the apparatus found on the abdomen. Figure No. 5 does not represent the " thoracic closing apparatus " as Krancher maintains, since the setae represented on the atrial wall and the beginning of the trachea are like those of a thoracic spiracle, whereas the lever is that of an abdominal spiracle. Krancher's account and figures are therefore confusing.

Alfonsus and Braun (1931), working on the internal structure of *Braula coeca* Nitzsch, gave two semi-schematic figures of the mesothorax and of an abdominal spiracle, without describing the regulatory apparatus. Their figures are moreover incomplete.

Melophagus ovinus (L.).

The Thoracic Spiracles.

The first thoracic spiracle (pl. XXII, fig. 1) of *M. ovinus* is situated at the upper edge of the pleuron between the first and second limb bases. The brown peritremal sclerite (PR) is round or slightly oval and encloses a wide spiracular opening leading to a large atrial chamber composed of two divisions. The first (AT_1) is funnel-shaped with a yellowish sclerotic wall, from which, as well as from the peritreme, arise a few alternating rows of long yellow hairs. These are unbranched and project into the cavity of the atrium, forming an efficient filtering apparatus (FA) similar to that found by Alfonsus and Braun (1931) in the mesothoracic spiracle of *Braula coeca.* The second division (AT_2) is a narrow membranous chamber, placed between the first part of the atrium and the tracheal mouth (TO) (*vide* text-fig. 14). At the junction between the two divisions of the atrium there is a sclerotised ring (pl. XXII, fig. 1 : SR and also figs. 2A and 2B of the second thoracic spiracle) which gives the second atrial opening a certain amount of support. The membranous wall of the second atrial chamber is strengthened by a few scattered elastic cuticular strands (pl. XXII, fig. 1 : S). Arising near the inner end of the second atrial chamber is an elastic ring (pl. XXII, figs. 1, 2A and 2B : R), which regulates the size of the aperture leading to the tracheae. Dorsally this ring is firmly attached to an inverted triangular sclerotised piece (pl. XXII, fig. 2A : TS) arising from the wall of the first atrial division, and passing along that of the second division



Text-fig. 14.—Schematic section of thoracic spiracle of *Melophagus ovinus.*

of the atrium. On the elastic ring (pl. XXII, figs. 2A and 2B : R) are some fine short hairs (H) projecting into the lumen of the membranous chamber. The sclerotic and the elastic ring mentioned above are also present, according to Alfonsus and Braun (1931), in the mesothoracic spiracle of *Braula coeca*. The second ring in *Braula* probably regulates the size of the tracheal opening as does the elastic ring in *M. ovinus*, although it was not so described by the above authors. A strong fan-shaped closing muscle (pl. XXII, figs. 1, 2A and 2B : CM), which has its broad base on a thick apodemal ridge (pl. XXII, figs. 1, 2A and 2B : RD) is inserted on the base of the elastic ring.

The regulatory apparatus consists of : (*a*) the elastic ring, and (*b*) the closing muscle. Contraction of the muscle draws the two sides of the ring together until the membranous wall of the atrium meet and close the opening between them. The elastic nature of the ring and the surrounding membranous wall cause the sides of the ring to separate as soon as the muscle relaxes and to leave the opening free.

The second thoracic spiracle (pl. XXII, figs. 2A and 2B) is situated on the pleuron between the basal articulations of the 2nd and 3rd leg. It is slightly smaller and rounder than the anterior spiracle. Other morphological characters as well as the structure and mechanism of regulation are the same as in the anterior thoracic spiracle.

The Abdominal Spiracles.

The abdominal spiracles (pl. XXII, figs. 3, 4, 5A and 5B) are small openings situated on the pleura and are surrounded by circular brown peritremes devoid of hairs. The peritremal sclerite merges into a spiral band (pl. XXII, fig. 3 : SBD) passing along a spindle-shaped atrium (AT), and tends to fade in places in the yellow cuticular wall of the latter. Proximally the atrial wall is membranous and is invested with elastic tissue fibres (pl. XXII, fig. 4 : EF). The spiral band divides just above the tracheal entrance into two (pl. XXII, fig. 3 : BD) which run opposite to one another in the membranous part of the atrium. One of these bands passes the head of a large L-shaped lever (pl. XXII, figs. 3, 4, 5A and 5B : L), which is situated to the side of the tracheal tube, and then joins the taenidia ; the other passes directly to the wall of the trachea and forms part of the regulatory apparatus. This band is held in position by the lateral body-wall muscles. The strongly sclerotised lever is moved by a rather broad muscle (CM) arising on its free curved end and inserted on the band close to the head of the lever. The insertion of this muscle, according to Krancher (1881), is on a small " chitinous " projection which stands on the tracheae opposite the lever. On contraction, the closing muscle pulls the free curved end of the lever upwards and thus presses the head of the latter against the opposite band. On muscle relaxation, the curved end of the lever drops down a little, and so comes to lie along the tracheal tube. As a result of this and of the elasticity of the proximal part of the atrium, the head of the lever is separated from the opposite band and leaves the tracheal mouth free.

It is seen from the above account that, as in other Diptera, the thoracic regulatory apparatus of *M. ovinus* differs in its structure and mechanism from that of the abdomen and is not the same as Krancher supposed.

DISCUSSION.

The conclusions to be drawn from the foregoing account of the thoracic and abdominal spiracular regulatory apparatus may be summarised as follows :

1. Two main types of regulatory apparatus in insects are recognised: (1) the external, and (2) the internal type. The external type is found in the Orthoptera (Krancher 1881 and Vinal 1919), in the metathorax of *Dytiscus* (Alt 1909), in the thorax of Hemiptera (Mammen 1912), and in the prothorax of *Apis* (Snodgrass 1925). In the course of the present work it was also found in Mecoptera, in the metathorax of Neuroptera and Trichoptera and in the thorax of most Nematocera. The internal type is divisible into (*a*) the flap type (thorax of TACHINIDAE and ANTHOMYIIDAE) and (*b*) the atrial or tracheal type (thorax of some Brachycera and Pupipara and all known types of abdominal regulatory apparatus).

2. The lids are more or less undifferentiated parts of the body wall, which may be raised slightly above the surface of the integument. The flaps and other types of internal apparatus, on the other hand, are more highly differentiated structures and may be situated at varying depths beneath the surface.

3. Those spiracles with one movable and one rigid lid may possibly represent a primitive condition. This shows the least advance on the condition found in Apterygota and Myriapoda and is found in the anterior thoracic spiracles of Orthoptera and Dermaptera (Krancher, Vinal, Snodgrass 1929).

4. When the closing muscle is inserted equally on the bases of the lids, both these are movable.

5. An intermediate stage is found in the posterior thoracic spiracle of Mecoptera, Neuroptera and Trichoptera where the movement of the lids is unequal.

6. The abdominal regulatory apparatus is always situated beneath the surface of the body and exhibits a wider range of variation in structure and mechanism than is found in the thoracic apparatus.

The above classification is applicable to all known types of spiracular regulatory apparatus. It differs from that of Snodgrass (1929 and 1935), who distinguished two types of "closing apparatus," external (thoracic), in which the closure is accomplished by means of the outer "lips" of the atrium, and internal (abdominal) in which the passage from the atrium into the trachea is blocked. This scheme, however, takes no account of the fact that the mechanism is internal in certain types of thoracic regulatory apparatus, the parts being homologous (in their positions relative to the external opening) with those of the abdominal apparatus of the lower Pterygota as well as of Mecoptera, Neuroptera and Trichoptera. In the case of *Melophagus ovinus*, indeed, the thoracic apparatus is situated still farther from the surface and, as in the highly developed abdominal apparatus, regulates the diameter of the passage between atrium and trachea. While in agreement with the distinction made by Snodgrass between two main categories of "closing apparatus," external and internal, the results of the present investigation show that these are not (as Snodgrass suggests) coextensive with the categories thoracic and abdominal. The classification proposed by Mammen (1912) is based on a study of the muscles of the "closing apparatus," their number and the nature of their attachments, but this author deals almost entirely with Hemiptera. In the light of the present work this classification appears of restricted utility. Krancher (1881), however, classified spiracles into two main groups based mainly on their external morphology.

Although the thoracic and abdominal apparatus often differ markedly in structure and mechanism, as mentioned before, it is possible to demonstrate that both could have been derived from a common prototype and that later in the process of evolution the abdominal apparatus may have diverged from the thoracic. As the thoracic and abdominal spiracles of Onychophora, Myriapoda and Thysanura are simple slits in the body wall with no provision for regulating the size of the opening, it is not unreasonable to suppose that, when it first made its appearance, the regulatory apparatus of the abdominal spiracles was similar to that of the thoracic ones. Evidence of this is provided by the following facts.

1. In the larval stages of Lepidoptera (Krancher 1881 and Snodgrass 1929) and other larvae (Snodgrass 1929), the regulatory apparatus is the same in both types of spiracles.

2. Among adult stages, the abdominal apparatus is the same as the thoracic in Odonata (Krancher 1881). In the case of *Dytiscus* (Alt 1909) the abdominal apparatus differs only slightly from that of the anterior thoracic spiracles.

3. The divergence between the abdominal and thoracic spiracles is least marked in those insects which on other grounds are regarded as most generalised. Thus, in the Orthoptera, for example, the main difference is that in the thoracic spiracle the body wall bulges outwards whereas in the abdominal type it is slightly invaginated. In both cases the same integumental parts form the regulatory apparatus. The description and figures given by Krancher (1881), Vinal (1919) and Snodgrass (1929) for Orthoptera, as well as the results of Mammen (1912) on Hemiptera and those of the present work on Mecoptera, Trichoptera and Neuroptera point without doubt to this conclusion.

4. Moreover, in many forms, especially most primitive ones, the mechanism for regulating the spiracular opening is essentially the same in both types of spiracles: in the anterior thoracic as well as the abdominal spiracles of Orthoptera, for example, one part of the body wall is movable while the other is rigid. The closing muscle has its attachment on a process of the movable lobe, and by its contraction draws this against the opposite rigid lobe, thus closing the aperture between them. Opening is accomplished by contraction of an opening muscle, and simultaneous relaxation of a closing muscle. The same mechanical principle is encountered in the Hemiptera (Mammen 1912), where in both thoracic and abdominal spiracles the movable part of the spiracular rim is drawn against the rigid portion by means of a closing muscle attached to a process at the base of the movable thoracic or abdominal lobe, whereas opening is accomplished through the elasticity of the movable lobe. In the abdominal apparatus, the above-mentioned process is more elongated and more rigid than that of the thoracic, and assumes a conical shape which perhaps affords a better attachment for the closing muscle. The more complex types of abdominal apparatus may have arisen in some such way as this by progressive modification of the simple type. Conceivably the increased development of the muscle itself has led to the production of the more effective levers and other similar parts found in the higher forms, since muscle tension may well be responsible for the development of apodemes and other skeletal structures in the region where the muscle is inserted into the cuticle (Wigglesworth 1939).

5. Finally, the function of the thoracic and abdominal regulatory apparatus may be the same as shown by Lee (1925 and 1927) and others in Orthoptera where the first four spiracles (the thoracic and the first two abdominals) are inspiratory.

As to the origin of the sclerotised parts of the abdominal regulatory apparatus, Krancher (1881) maintained that in both the simple and the more complex closing apparatus the parts are local thickenings of the spiral fibre of the trachea. That Krancher's hypothesis is erroneous can be proved by examination of a less differentiated regulatory apparatus such as that of the Orthoptera, where the parts are clearly nothing more than invaginations of the body wall. Even in more evolved types of apparatus where a lever is present at the site of the opening, as is the case in Mecoptera (p. 110) and Neuroptera (p. 112), it can be easily seen that the lever and other cuticular parts are continuations of the inflected peritreme or similar sclerotised regions of the body wall. Passing on to yet more complex forms of apparatus where the lever is situated at the inner end of a well-developed atrium, it can be seen that the same principle still holds. In RHYPHIDAE, for example (pl. VII, figs. 3, 4A and 4B), the sclerotised lever is continuous with the bands which pass inwards from the cuticle or the peritremal sclerite, along the atrial wall. Even the so-called bridge, specifically mentioned by Krancher as formed of a number of fused tracheal spirals, can be seen in sections as well as in whole mounts, to be in fact a part of the sclerotised spiral thickening of the atrium. The findings of Alt (1909) in *Dytiscus* and of Mammen (1912) in Hemiptera are in agreement with the conclusions of the writer concerning the derivation of the parts of the regulatory apparatus from the integument.

While the muscles of the regulatory apparatus vary considerably in size and mode of attachment in different families, yet with respect to the arrangement of the bundles they fall into two types: (*a*) those in which the bundles are parallel, and (*b*) those in which the bundles radiate fanwise from a centre.

In Orthoptera (Krancher 1881 and Snodgrass 1929), Odonata (Krancher 1881) and Hemiptera (Mammen 1912) the thoracic and abdominal muscles are of the same type, the bundles being parallel in Orthoptera and radiating in Odonata and Hemiptera. In the present investigation thoracic and abdominal muscles were found to differ. The thoracic spiracles of Mecoptera and Diptera usually have a fan-shaped muscle, while in the abdominal spiracles the bundles are more or less parallel. In the Neuroptera and Trichoptera, on the other hand, the anterior as well as the abdominal muscles are of the parallel-bundle type, having a spindle and semi-circular shape in the anterior thoracic and abdominal spiracles of Trichoptera respectively. The posterior thoracic spiracular muscles of the last two orders are of the radiate type. It was observed in the course of this work that the regulatory muscles always originate in the segment containing the spiracle and that when the closing muscle of the abdominal apparatus of *Chironomus dorsalis* (p. 118) is fully relaxed, it has the same appearance as those in its immediate neighbourhood. This suggests that the closing muscle of *Chironomus dorsalis* may be homologous with the lateral body-wall muscles, but the points of attachment may have shifted on to the regulatory apparatus. A more or less similar view was put forward by Solowiow (1910) for Lepidoptera, and by Mammen (1912) for Hemiptera.

Perhaps one of the most striking adaptations of the spiracular apparatus to different modes of life is its tendency to become internal and to be protected by " filter " or " basket apparatus." The purpose of the internal position of the apparatus and the filter mechanism may be twofold: (*a*) to prevent the entry of foreign matter, either solid particles or water, or (*b*) to cut down water loss by altering the gradient of diffusion of water vapour from the surface of the spiracle.

As to the prevention of entry of foreign matter, it is found that *Melophagus ovinus*, for example, possesses an effective mechanism for filtering the air passing into the tracheal system. In *M. ovinus* the spiracular opening as well as the well-developed atrium is guarded by rows of long stiff hairs (p. 145) between which solid particles of various sizes were found to be entangled. The hairs as well as the spiracular region, moreover, by virtue of their hydrofuge property prevent the entry of water into the tracheal system. That glandular cells occur in association with such hairs and around the spiracular region is shown by Lowne (1890–92) in adult *Calliphora erythrocephala* and by the work of Keilin (1913) and Keilin, Tate and Vincent (1935) on the perispiracular glands of larval Diptera. The last three authors found that such glands were responsible for the production of an oily secretion which prevents the wetting of the spiracle. In contrast to the hydrofuge property of the above-mentioned hairs, those protecting the spiracles of the petroleum fly, *Psilopa petrolei* Coq. are presumably coated with a hydrophilic substance (Thorpe 1930) which prevents the oil from spreading into the tracheal system.

The sinking of the regulatory apparatus below the surface of the body and the presence of a filter of interlacing hairs result in the formation of a pocket of relatively still air of a relatively high humidity in the immediate vicinity of the spiracular opening. The effect of this will be to reduce the steepness of the humidity gradient along the trachea to the spiracular opening, and hence to reduce the rate of water loss from the tracheal system. This device is entirely comparable to the dense covering of hairs on the surface of the leaves of xerophytes, whereby a layer of still air of relatively high humidity is maintained over the surface of the leaf. In support of this contention, Bergold (1934), working on the spiracles of xerophilous and hydrophilous beetles, came to the conclusion that in the former the stigmata are small, sunk in a pit below the surface of the body, and provided with a basket-like apparatus of dense interlacing hairs; in the latter, however, these adaptations are absent. It was found during the present investigation that the filter apparatus is well developed in those forms that inhabit dry places and in actively flying forms, such as BOMBYLIIDAE, SYRPHIDAE, ANTHOMYIIDAE and TACHINIDAE. Unlike forms such as these, insects confined to damp places, as are most of the nematocerous Diptera investigated, do not possess a filter arrangement.

The nomenclature of the parts of the regulatory apparatus first proposed by Landois and Thelen (1881) and subsequently adopted by later workers applies only to the more highly differentiated types of apparatus, *e.g.* the lever type of the Cyclorrhapha and similar forms. As Babák (1921) has pointed out, it is inconvenient to use these terms for parts which may indeed be homologous but which are quite different in form. In such cases a name should be given according to the shape and the function, if possible, of the part concerned. Until a detailed study of the apparatus in all the orders of insects has been made, it is inadvisable to attempt a uniform system of nomenclature.

The present investigation adds to the list of characters common to members of the panorpoid complex. Thus it has been observed that the regulatory apparatus of the second thoracic spiracle is remarkably similar in Mecoptera, Neuroptera and Trichoptera. Moreover, in both Mecoptera and Neuroptera the abdominal apparatus is almost identical with that of larval Lepidoptera as described and figured by Krancher (1881), while that of Trichoptera is different and appears more generalised. In adult Lepidoptera (Krancher 1881), though the apparatus is similar to that of the larva, it lies still farther below the surface of the body, and the opening muscle disappears altogether. In adult Diptera, also, the opening muscle is absent and the elasticity of the deformable parts of the apparatus counteracts the force of the closing muscle. These conclusions afford additional evidence of the affinities of Mecoptera, Neuroptera and Lepidoptera. Judging from the structure of their highly developed abdominal regulatory apparatus alone, these three orders constitute a group within the panorpoid complex from which both Trichoptera and Diptera are somewhat removed.

Summary.

1. An illustrated account is given of a comparative study of the spiracular regulatory apparatus of Mecoptera, Neuroptera, Trichoptera and Diptera.

2. The Thysanura and other Apterygota have no means of regulating the size of the spiracular opening. Both thoracic and abdominal spiracles are simple openings, leading directly to the tracheal system.

3. The types of regulatory apparatus found among insects are divisible into two main groups: (1) an external, and (2) an internal type. While both these groups are of common occurrence in the thoracic spiracles, the internal apparatus is typical of the abdominal ones. It is always situated below the surface of the body at the atrial or tracheal entrance. According to its structure and mechanism it may be divided into (*a*) the flap type, and (*b*) the atrial or tracheal type.

4. Possibly the external or lid type of apparatus represents a primitive device for regulating the spiracular opening. Three variants can be recognised: (*a*) in which one lid only is movable, (*b*) in which both lids move but not to the same extent, and (*c*) in which both lids are equally movable.

5. Evidence is advanced which, together with that from previous work, suggests that primitively one type of apparatus was common to both the thoracic and abdominal spiracles. Subsequently, the structure of the abdominal regulatory apparatus diverged from that of the thoracic.

6. The sclerotised parts of the abdominal regulatory apparatus are inflected regions of the body wall which may be greatly modified in forms such as Diptera.

7. The muscles of the regulatory apparatus may assume (*a*) a parallel, or (*b*) a fan shape. It is possible that these muscles did not evolve *de novo*; conceivably the lateral body-wall muscles may have become secondarily attached to the apparatus and thus regulate, by their contraction and relaxation, the size of the stigmatic or tracheal opening.

8. In actively flying insects as well as in those that inhabit dusty or dry environments, the thoracic regulatory apparatus is of the internal type and is always covered by a highly developed filter mechanism. The function of the latter may be twofold, (*a*) to exclude foreign matter, or (*b*) to reduce excessive water loss in some such way as by altering the gradient of diffusion of water vapour from the surface of the spiracle.

9. Within the panorpoid complex the Diptera and Trichoptera show least relation to the others.

10. It is pointed out that connective tissue, in which either white or yellow fibres predominate, as well as fibrous sheaths, exist around the spiracular opening and the regulatory apparatus. This problem requires a more detailed histological study and is, therefore, left for future consideration.

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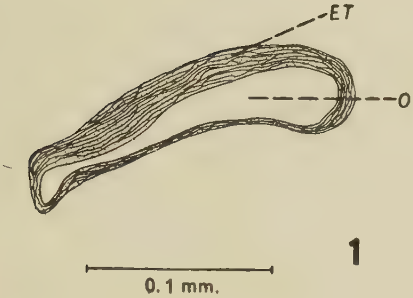
Plate I.

Thysanura.

Fig. 1. *Machilis* sp. Anterior thoracic spiracle, internal view.
2. *Machilis* sp. Transverse section showing one half of the posterior thoracic spiracle.
3. *Lepisma saccharina* L. Abdominal spiracle, internal view.
4. *Lepisma saccharina* L. Transverse section of an abdominal spiracle.
5. *Japyx* sp. Transverse section of an abdominal spiracle.

Key to lettering.

CT—Connective tissue: ET—Elastic tissue: H—Hairs: O—Opening: R—ing: TC—Tracheal cells.



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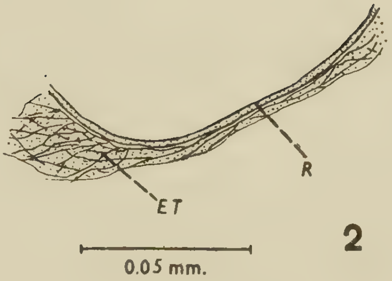

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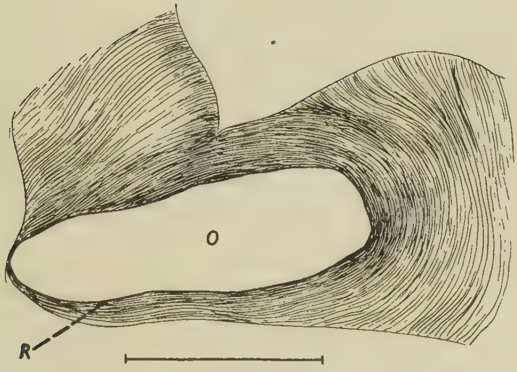

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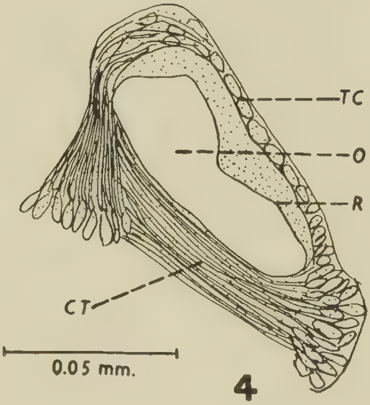
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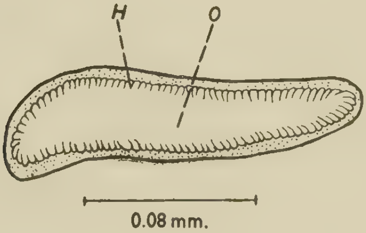

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PLATE II.

Mecoptera.

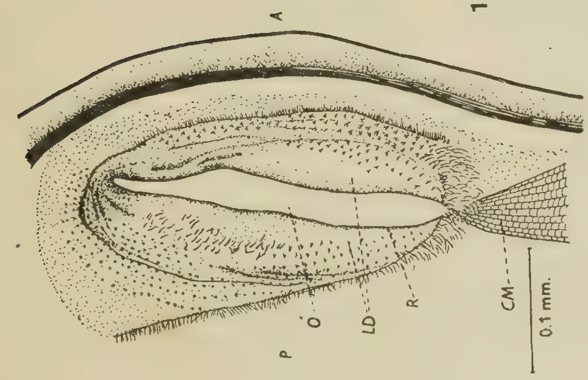
Panorpa communis L.

FIG. 1. Anterior thoracic spiracle, internal view—open.
2. Posterior thoracic spiracle, internal view—closed.
3. Abdominal spiracle, internal view—open.
4. Lever, band and elastic membrane with a part of the tracheae of an abdominal spiracle (dissected out) to show the relation between the above-mentioned parts.
5. Longitudinal section of an abdominal spiracle at the level of the regulatory apparatus.

FIGS. 6A and B. Abdominal spiracle in the open and closed positions (schematic).

Key to lettering.

A—Anterior : APR—Anterior border of peritreme : BD—Band : CM—Closing muscle : L—Lever : LD—Lid : MB—Membrane : O—Spiracular opening : OM—Opening muscle : P—Posterior : PR—Peritreme : PT—Plate : TN—Taenidia.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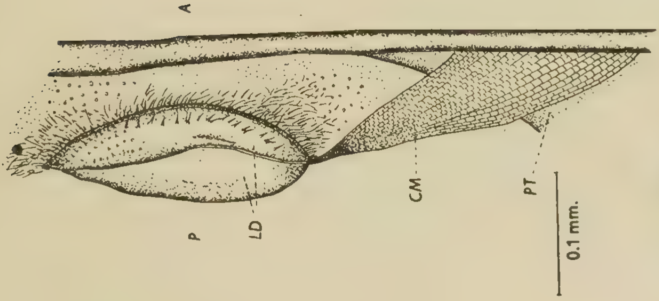
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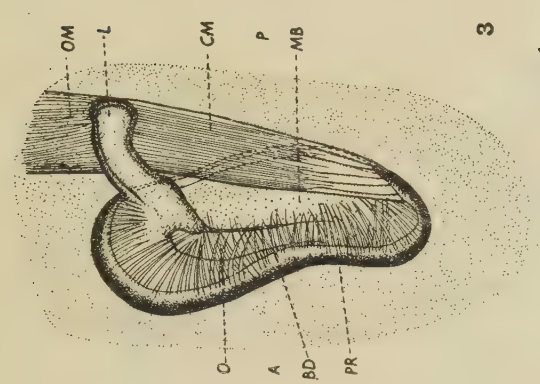
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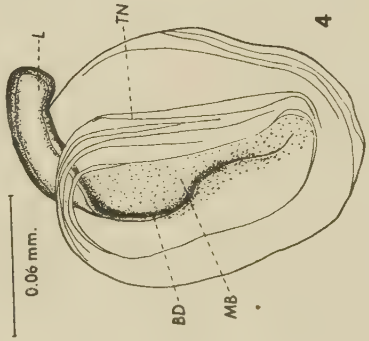
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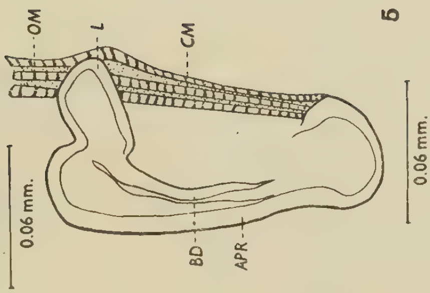
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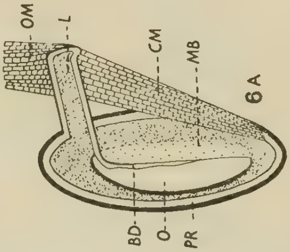
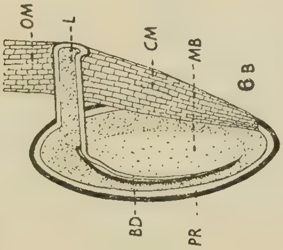
0.06 mm.

5


OM
L
CM
MB
BD
O
PR

6 A


OM
L
CM
MB
BD
PR

6 B

PLATE III.

CHIRONOMIDAE.

Chironomus dorsalis Fab.

FIG. 1. Anterior thoracic spiracle, external view—closed.
2. Posterior thoracic spiracle, internal view—open.
3. Abdominal spiracle, external view—open.
4. Abdominal spiracle, internal view—half open.
5. Abdominal spiracle, internal view—closed.

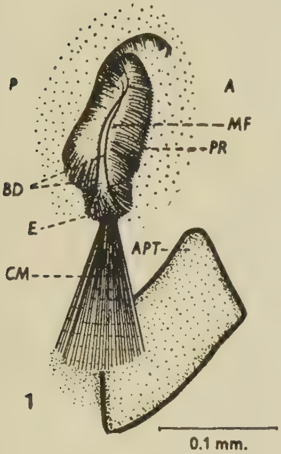
PSYCHODIDAE.

Psychoda sp.

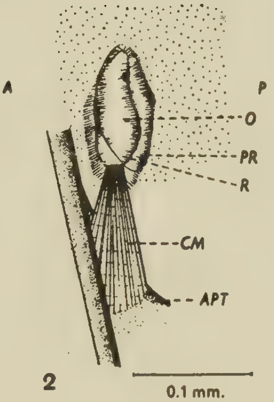
FIG. 6. Anterior thoracic spiracle, external view—open.
7. Posterior thoracic spiracle, internal view—open.
8. Abdominal spiracle, internal view—closed.

Key to lettering.

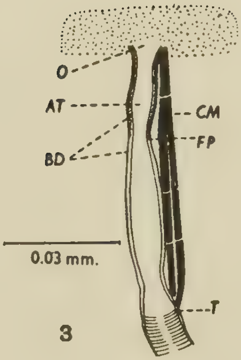
A—Anterior: APT—Apodemal plate: AT—Atrium: BD—Band: CM—Closing muscle: E—Elastic plate: F—Fold: FP—Flexible point: O—Spiracular opening: P—Posterior: PR—Peritreme: PT—Plate: R—Ring: RD—Ridge: T—Taenidia: MF—Membranous flaps.


P
A
MF
PR
BD
E
APT
CM
0.1 mm.

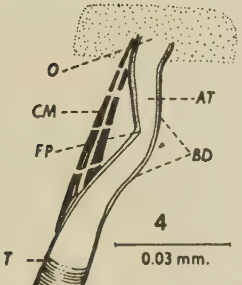
1


A
P
O
PR
R
CM
APT
0.1 mm.

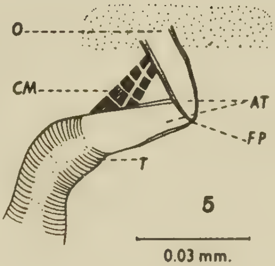
2


O
AT
CM
FP
BD
0.03 mm.
T

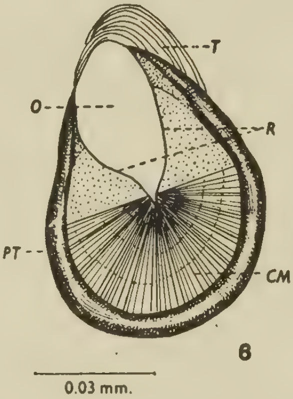
3


O
CM
AT
FP
BD
T
0.03 mm.

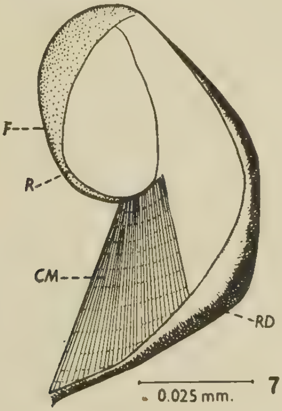
4


O
CM
AT
FP
T
0.03 mm.

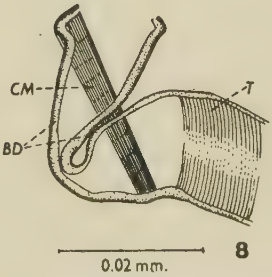
5


T
O
R
PT
CM
0.03 mm.

6


F
R
CM
RD
0.025 mm.

7


CM
T
BD
0.02 mm.

8

PLATE IV.

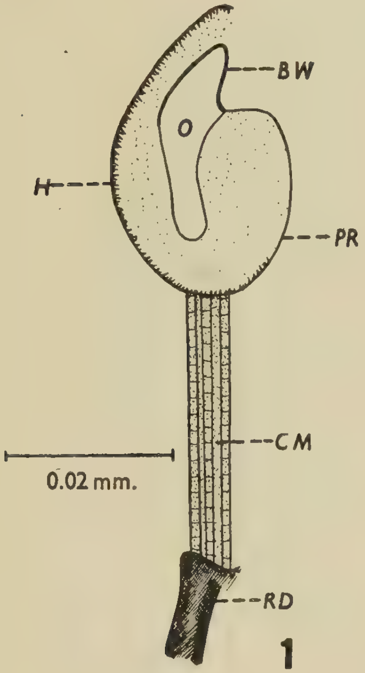
MYCETOPHILIDAE.

Sciara sp.

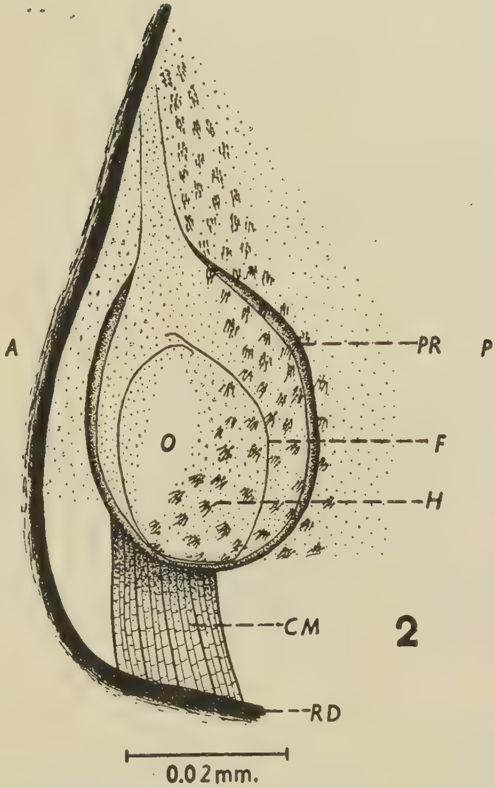
FIG. 1. Transverse section of the anterior thoracic spiracle.
2. Posterior thoracic spiracle, external view—open.
3. Transverse section of the posterior thoracic spiracle at the level of the regulatory apparatus.
4. Longitudinal section of an abdominal spiracle—open.

Key to lettering.

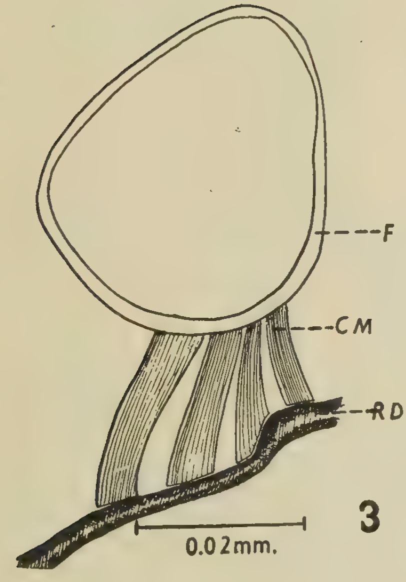
A—Anterior : AT_1—First atrial division : AT_2—Second atrial division : BW—Bow : CM—Closing muscle : F—Fold : H—Hairs : O—Spiracular opening : P—Posterior : PR—Peritreme : RD—Ridge : TO—Tracheal opening : TT—Tracheal tube.


BW
O
H
PR
CM
0.02 mm.
RD

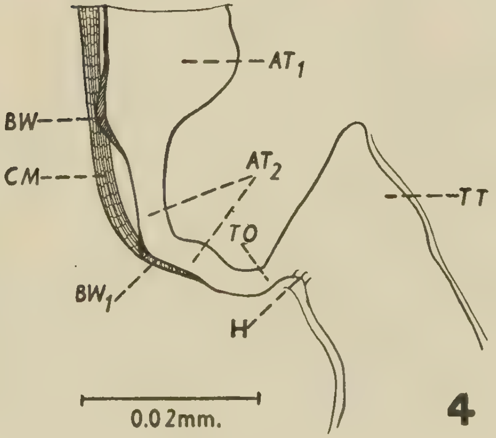
1


A
PR
P
O
F
H
CM
RD
0.02mm.

2


F
CM
RD
0.02mm.

3


AT1
BW
AT2
CM
TO
TT
BW1
H
0.02mm.

4

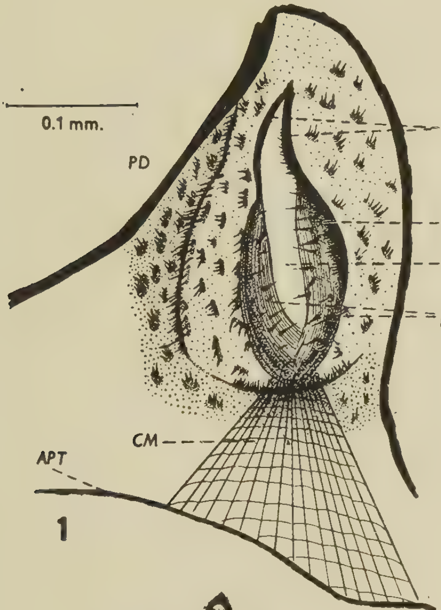
PLATE V.

Bibio hortulanus L.

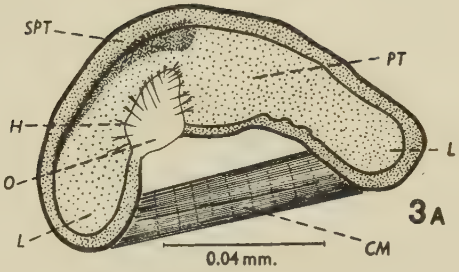
FIG. 1. Anterior thoracic spiracle, external view—open.
2. Posterior thoracic spiracle, external view—closed.
3A. Abdominal spiracle, internal view—open.
3B. Abdominal spiracle, internal view—closed.
FIGS. 4A and B. Serial transverse sections through the regulatory apparatus of an abdominal spiracle.

Key to lettering.

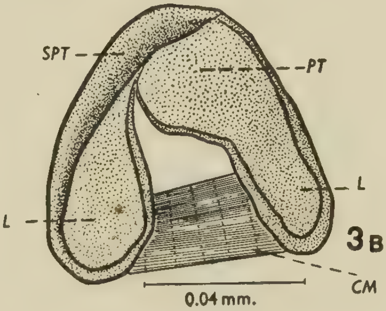
A—Anterior : APT—Apodemal plate : AV—Antero-ventral : BD—Band : CM—Closing muscle : CT—Connective tissue : F—Fold : H—Hairs : L—Lever : LD—Lid : O—Spiracular opening : P—Posterior : PD—Postero-dorsal : PR—Peritreme : PT—Plate : R—Ring : SPT—Densely sclerotised part of the plate : T—Taenidia : TO—Tracheal opening.


0.1 mm.
PD
F
A V
H
O
LD
CM
APT

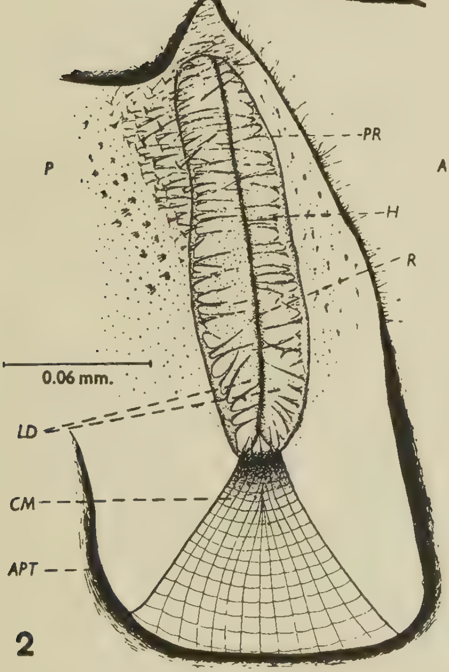
1


SPT
PT
H
L
O
L
CM
0.04 mm.

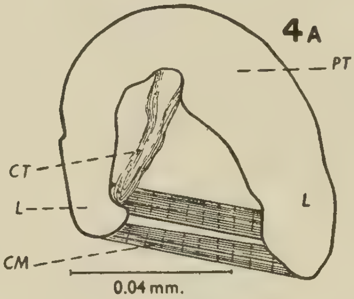
3A


SPT
PT
L
L
CM
0.04 mm.

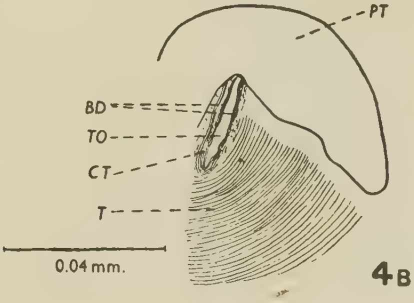
3B


PR
P
A
H
R
0.06 mm.
LD
CM
APT

2


PT
CT
L
L
CM
0.04 mm.

4A


PT
BD
TO
CT
T
0.04 mm.

4B

PLATE VI.

TIPULIDAE.

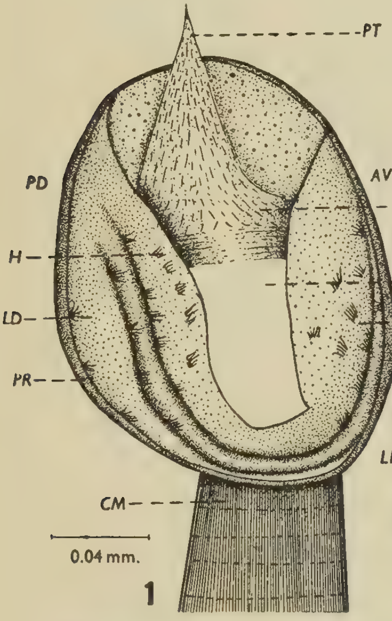
Tipula sp.

FIG. 1. Anterior thoracic spiracle, external view—open.
2. Anterior thoracic spiracle, internal view—open.
3. Posterior thoracic spiracle, internal view—open.
4. Lateral view of the regulatory apparatus of the posterior thoracic spiracle (lids are stretched).

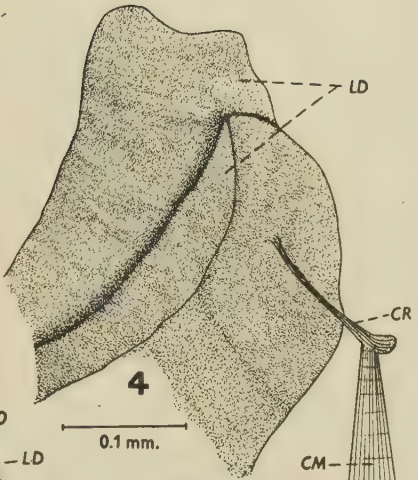
FIGS. 5A, B. Abdominal spiracles in the open and closed positions, inner view.

Key to lettering.

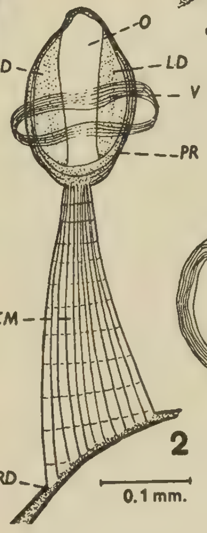
A—Anterior : AV—Antero-ventral : BD—Band : C—Collar : CM—Closing muscle : CR—Calliper : EBD—Elastic band : EF—Elastic fibres : F—Fold : H—Hairs : LD—Lid : O—Spiracular opening : PD—Postero-dorsal : PL—Pleura : PR—Peritreme : PT—Plate : RD—Ridge : TO—Tracheal opening : V—Vestibule.


PT
PD
AV
V
H
O
LD
LD
PR
CM
0.04 mm.

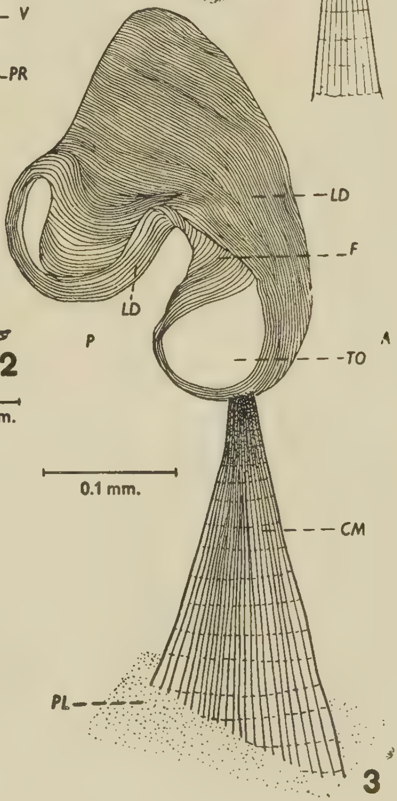
1


LD
CR
0.1 mm.

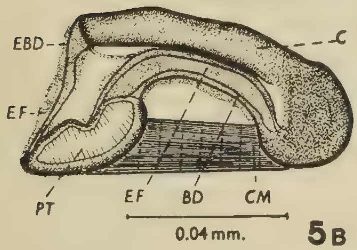
4


O
LD
LD
V
PR
CM
RD
0.1 mm.

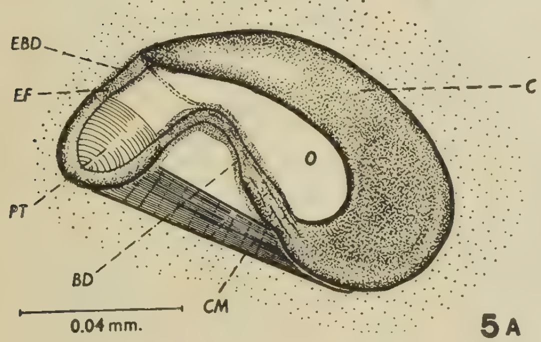
2


CM
LD
F
LD
P
A
TO
0.1 mm.
CM
PL

3


EBD
C
EF
PT
EF
BD
CM
0.04 mm.

5B


EBD
EF
C
O
PT
BD
CM
0.04 mm.

5A

PLATE VII.

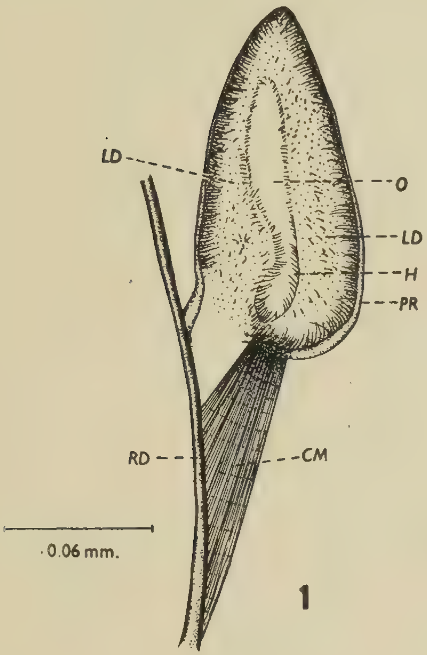
RHYPHIDAE.

Anisopus fenestralis (Scop.).

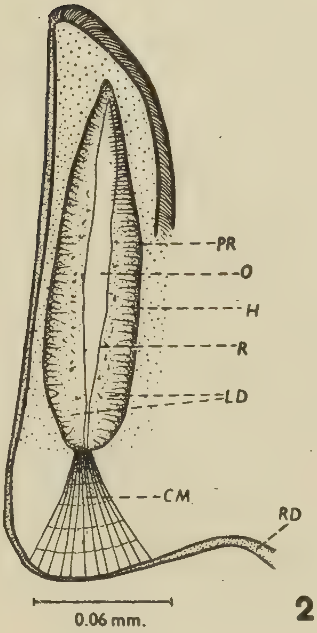
FIG. 1. Anterior thoracic spiracle, external view—open.
2. Posterior thoracic spiracle, external view—open.
3. Abdominal spiracle, internal view—open.
FIGS. 4A and B. Serial longitudinal sections of an abdominal spiracle—closed.

Key to lettering.

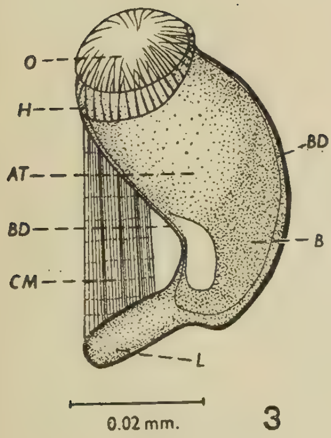
AT—Atrium : B—Bridge : BD—Band : CM—Closing muscle : H—Hairs : L—Lever : LD—Lid : O—Spiracular opening : PR—Peritreme : R—Ring : RD—Ridge : TT—Tracheal tube.


LD
O
LD
H
PR
RD
CM
0.06 mm.

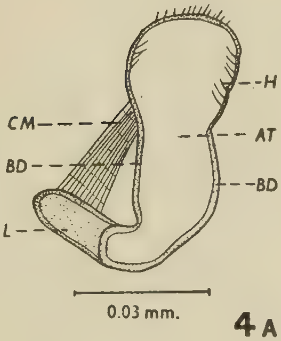
1


PR
O
H
R
LD
CM
RD
0.06 mm.

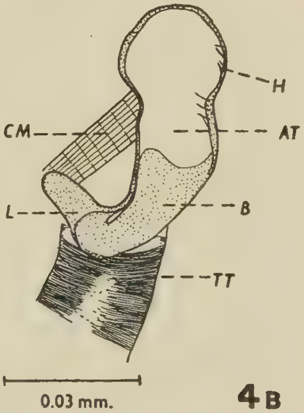
2


O
H
AT
BD
CM
BD
B
L
0.02 mm.

3


CM
BD
L
H
AT
BD
0.03 mm.

4 A


H
CM
AT
L
B
TT
0.03 mm.

4 B

PLATE VIII.

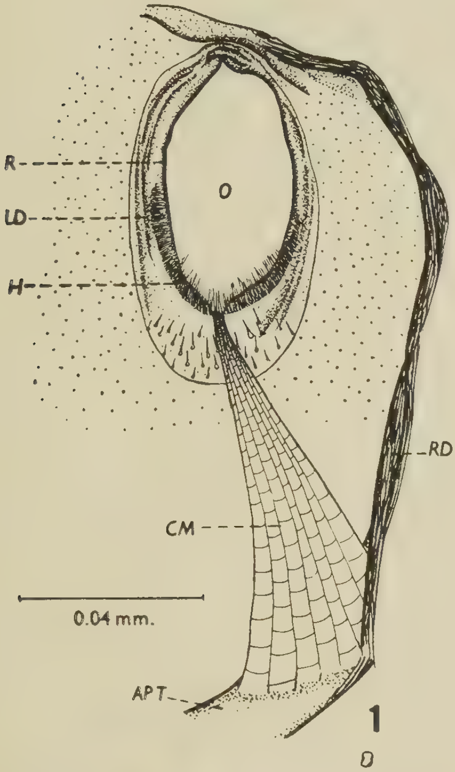
SIMULIIDAE.

Simulium sp.

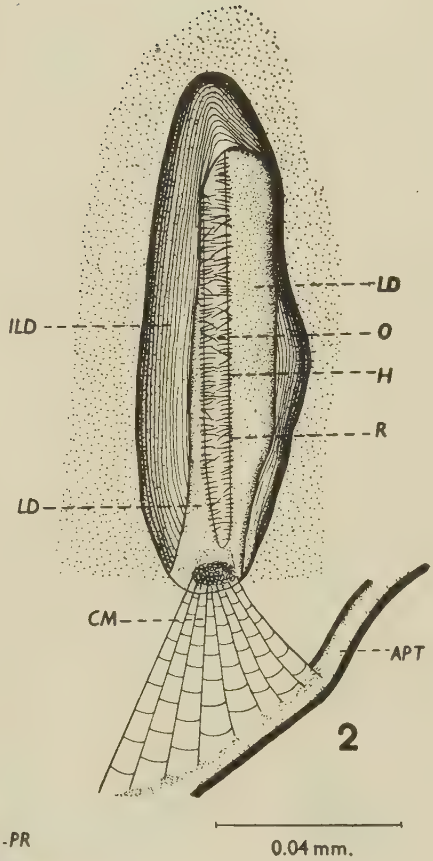
FIG. 1. Anterior thoracic spiracle, internal view—open.
2. Posterior thoracic spiracle, internal view—open.
3A. Abdominal spiracle, internal view—open.
3B. Abdominal spiracle, internal view—closed.
4. Transverse section of an abdominal spiracle through the regulatory apparatus.

Key to lettering.

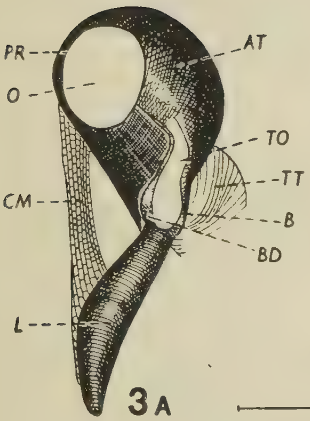
APT—Apodemal plate : AT—Atrium : B—Bridge : BD—Band : CM—Closing muscle : EF—Elastic fibres : H—Hairs : ILD—Inner inflection of lids : L—Lever : LD—Lid : O—Spiracular opening : PR—Peritreme : R—Ring : RD—Ridge : TO—Tracheal opening : TT—Tracheal tube.


R
LD
H
O
RD
CM
APT
0.04 mm.
D

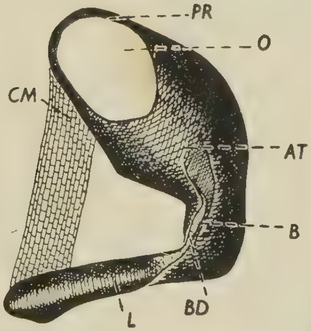
1


ILD
LD
O
H
R
LD
CM
APT
0.04 mm.

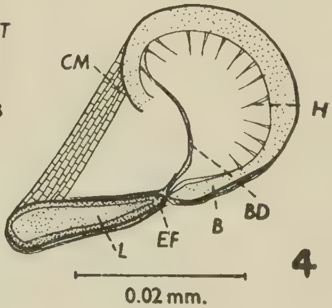
2


PR
AT
O
TO
TT
CM
B
BD
L
0.02 mm.

3A


PR
O
CM
AT
B
L
BD

3B


CM
H
BD
B
EF
L
0.02 mm.

4

PLATE IX.

CULICIDAE.

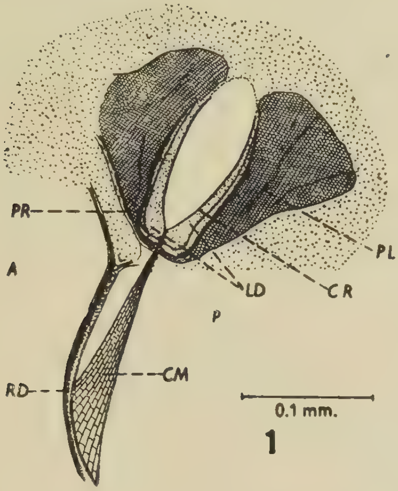
Anopheles maculipennis (Mg.).

FIG. 1. Anterior thoracic spiracle, internal view—open.
2. Posterior thoracic spiracle, external view—open.
3. Posterior thoracic spiracle (after Alessandrini and Missiroli 1926).
4. Abdominal spiracle, inner view—open.
5. Abdominal spiracle, inner view—closed.

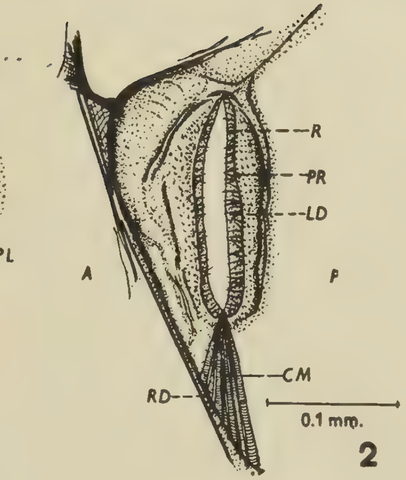
FIGS. 6A, B and C. Abdominal spiracles, open; half-open and closed (after Alessandrini and Missiroli 1926).

Key to lettering.

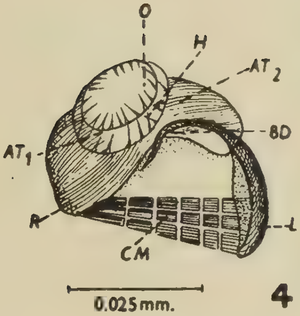
A—Anterior : AT_1—First atrial division : AT_2—Second atrial division : BD—Band : CM—Closing muscle : CR—Calliper : H—Hairs : K—Knob-like process : L—Lever : LD—Lid : O—Spiracular openings : P—Posterior : PL—Pleura : PR—Peritreme : R—Ring : RD—Ridge : T—Taenidia : TO—Tracheal opening.


PR
A
PL
LD
CR
P
CM
RD
0.1 mm.

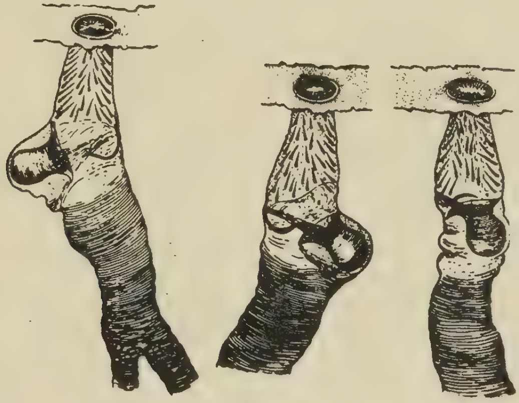
1


R
PR
LD
A
P
CM
RD
0.1 mm.

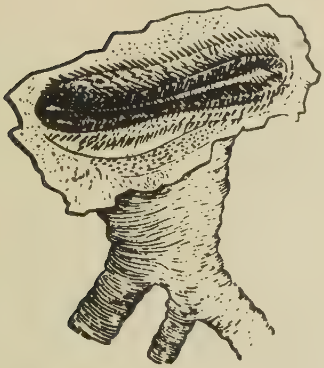
2


O
H
AT2
BD
AT1
R
L
CM
0.025 mm.

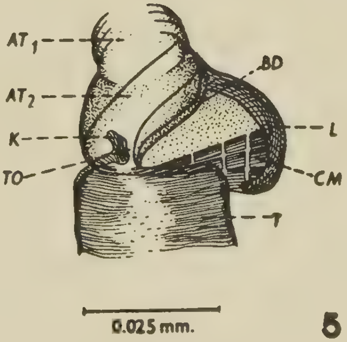
4



6A 6B 6C



3


AT1
AT2
K
TO
BD
L
CM
T
0.025 mm.

5

PLATE X.

Anopheles maculipennis (Mg.).

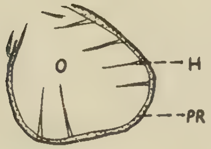
FIGS. 1A, B, C, D and E. Serial transverse sections of an abdominal spiracle showing the regulatory apparatus.

Theobaldia annulata (Schrank).

FIG. 2. External opening of an abdominal spiracle.
3. Regulatory apparatus of same.

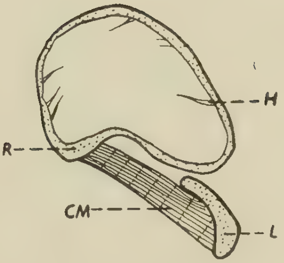
Key to lettering.

AT—Atrium : CM—Closing muscle : H—Hairs : K—Knob-like process : L—Lever : O—Spiracular opening : PR—Peritreme : R—Ring.

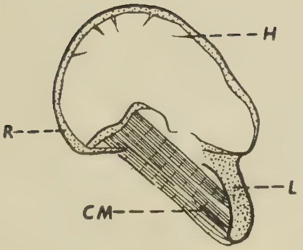


1A

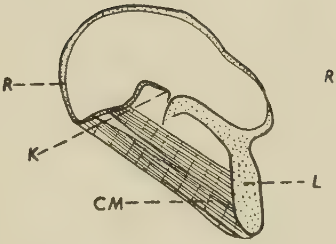
0.025 mm.



1B

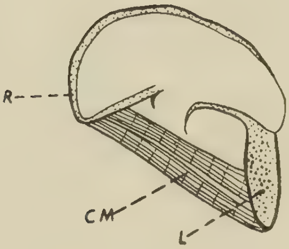


1C

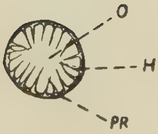


1D

0.025 mm.

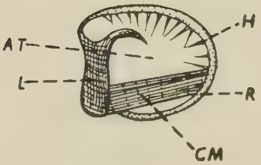


1E



2

0.025 mm.



3

PLATE XI.

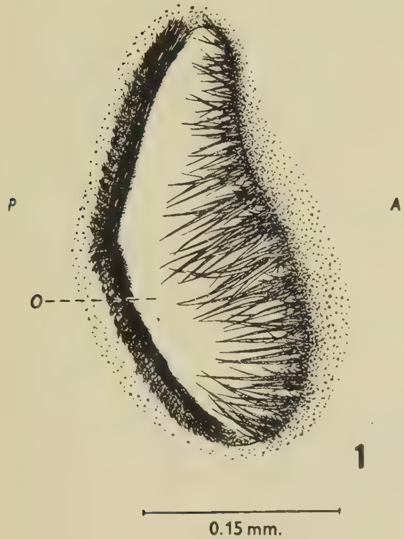
BOMBYLIIDAE.

Bombylius major L.

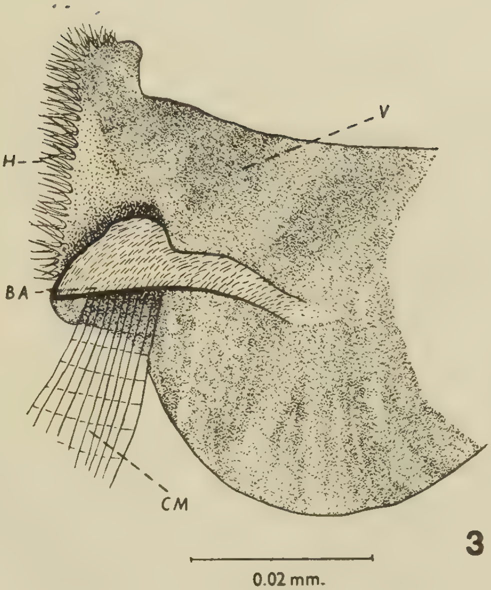
FIG. 1. Anterior thoracic spiracle, external view.
2. Anterior thoracic spiracle, internal lateral view to show the regulatory apparatus.
3. Posterior thoracic spiracle, internal lateral view to show the regulatory apparatus.
4. Abdominal spiracle, external view showing the stigmatic opening and the regulatory apparatus.

Key to lettering.

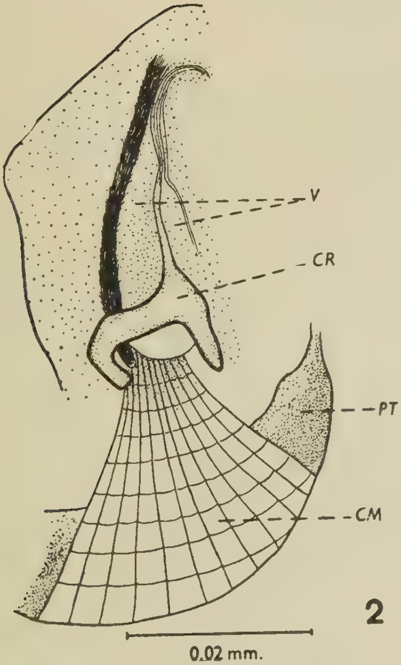
A—Anterior: At—Atrium: BA—Bar: C—Collar: CM—Closing muscle: CR—Calliper: E—Elastic plate or connection: EBD—Elastic band: H—Hairs: N—Manubrium: O—Spiracular opening: P—Posterior: PT—Plate: V—Vestibule.


P
A
O
0.15 mm.

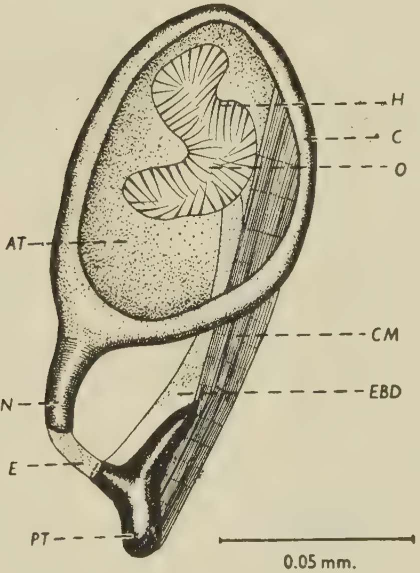
1


V
H
BA
CM
0.02 mm.

3


V
CR
PT
CM
0.02 mm.

2


H
C
O
AT
CM
EBD
N
E
PT
0.05 mm.

4

PLATE XII.

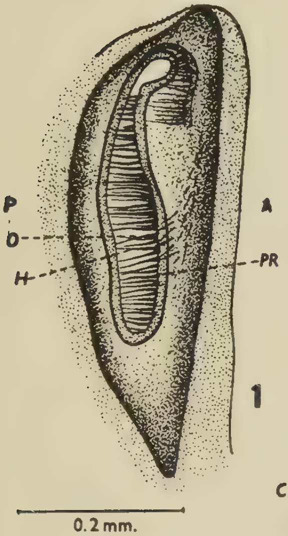
ASILIDAE.

Leptogaster cylindrica (Deg.).

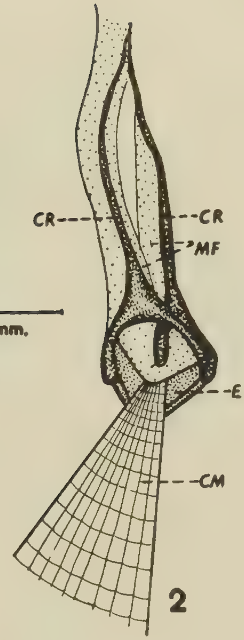
FIG. 1. Anterior thoracic spiracle, external view.
2. Regulatory apparatus of the anterior thoracic spiracle.
3. Posterior thoracic spiracle, external view.
4. Regulatory apparatus of the posterior thoracic spiracle.
5. Abdominal spiracle, internal view—open.

Key to lettering.

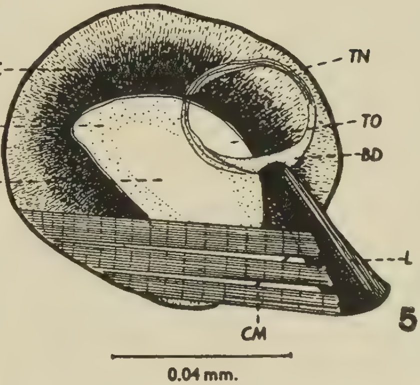
A—Anterior: BD—Band: C—Collar: CM—Closing muscle: CR—Calliper: E—Elastic plate: H—Hairs: L—Lever: MF—Membranous flap: MS—Narrow membranous strip: O—Spiracular opening: P—Posterior: PR—Peritreme: RD—Ridge: TN—Taenidia: TO—Tracheal opening.


P
A
O
H
PR
0.2 mm.

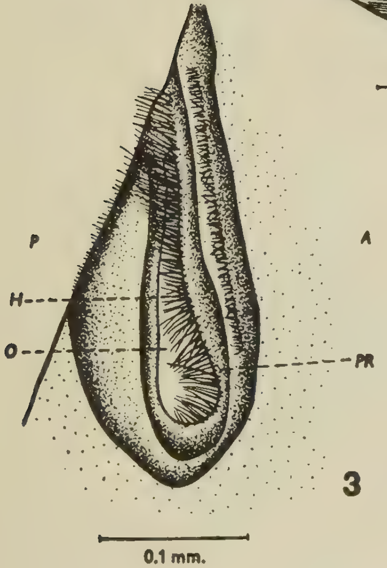
1


CR
CR
MF
0.1 mm.
E
CM

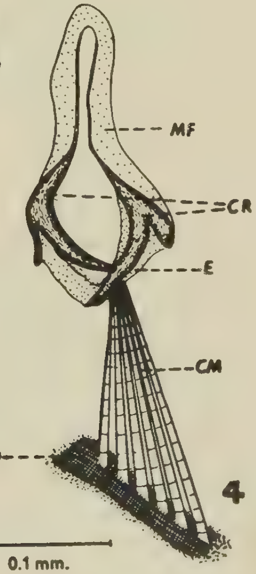
2


C
MS
O
TN
TO
BD
L
CM
0.04 mm.

5


P
A
H
O
PR
0.1 mm.

3


MF
CR
E
CM
RD
0.1 mm.

4

PLATE XIII.

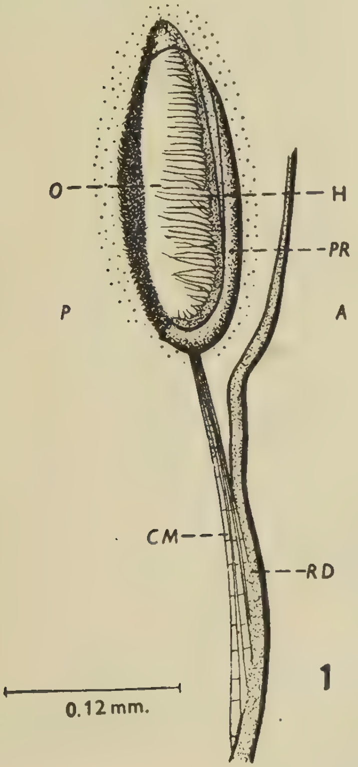
DOLICHOPODIDAE.

Dolichopus festivus Haliday.

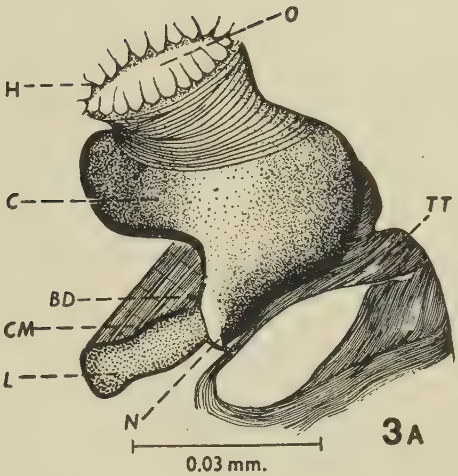
FIG. 1. Anterior thoracic spiracle, external view—open.
2. Posterior thoracic spiracle, internal view—open.
3. Abdominal spiracle, internal view—open.
3A. Abdominal spiracle, internal view—closed.

Key to lettering.

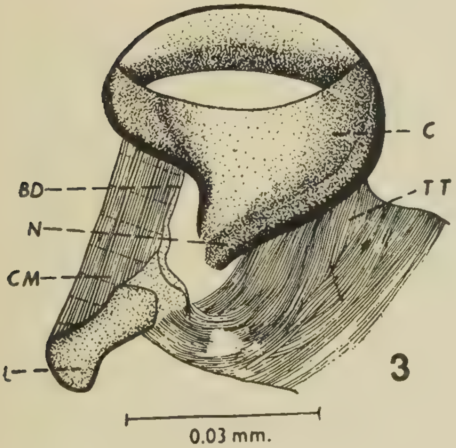
A—Anterior: BD—Band: C—Collar: CM—Closing muscle: H—Hairs: L—Lever: M—Manubrium: O—Spiracular opening: P—Posterior: PR—Peritreme: R—Ring: RD—Ridge: TT—Tracheal tube.


O
H
PR
P
A
CM
RD
0.12 mm.

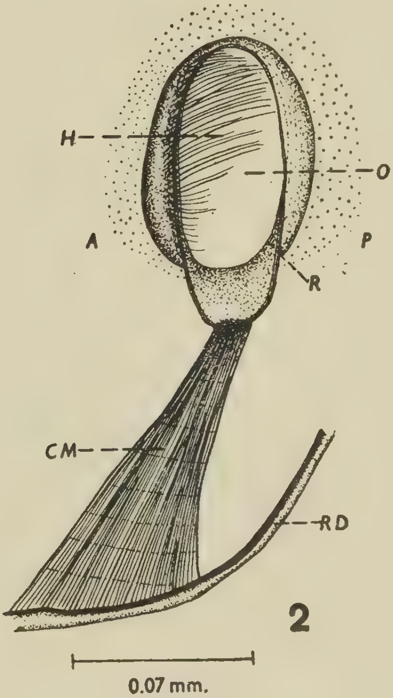
1


O
H
C
TT
BD
CM
L
N
0.03 mm.

3A


C
BD
TT
N
CM
L
0.03 mm.

3


H
O
A
P
R
CM
RD
0.07 mm.

2

PLATE XIV.

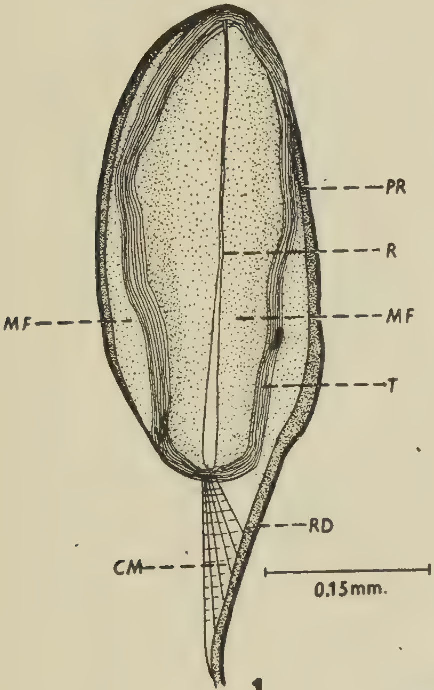
EMPIDAE.

Empis livida L.

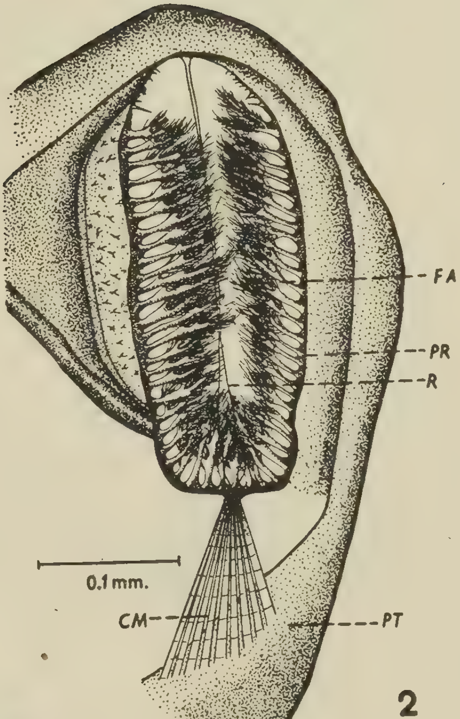
FIG. 1. Anterior thoracic spiracle, internal view—closed.
2. Posterior thoracic spiracle, external view—closed.
3. Abdominal spiracle, internal view—open.

Key to lettering.

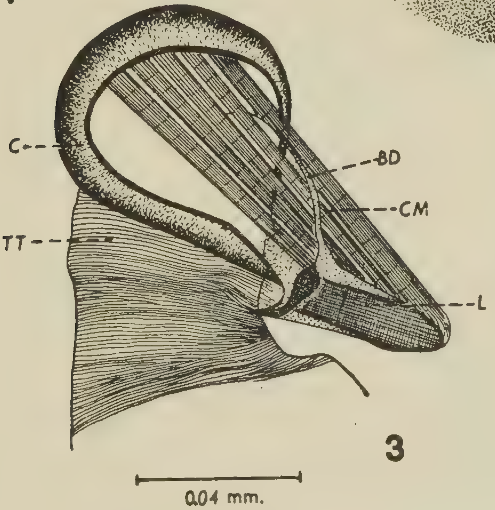
BD—Band: C—Collar: CM—Closing muscle: FA—Filter apparatus: L—Lever: MF—Membranous flap: PR—Peritreme: PT—Plate: R—Ring: T—Taenidia: TT—Tracheal tube.


PR
R
MF
MF
T
RD
CM
0.15mm.

1


FA
PR
R
0.1mm.
CM
PT

2


C
BD
CM
TT
L
0.04 mm.

3

PLATE XV.

Rhingia campestris (Mg.).

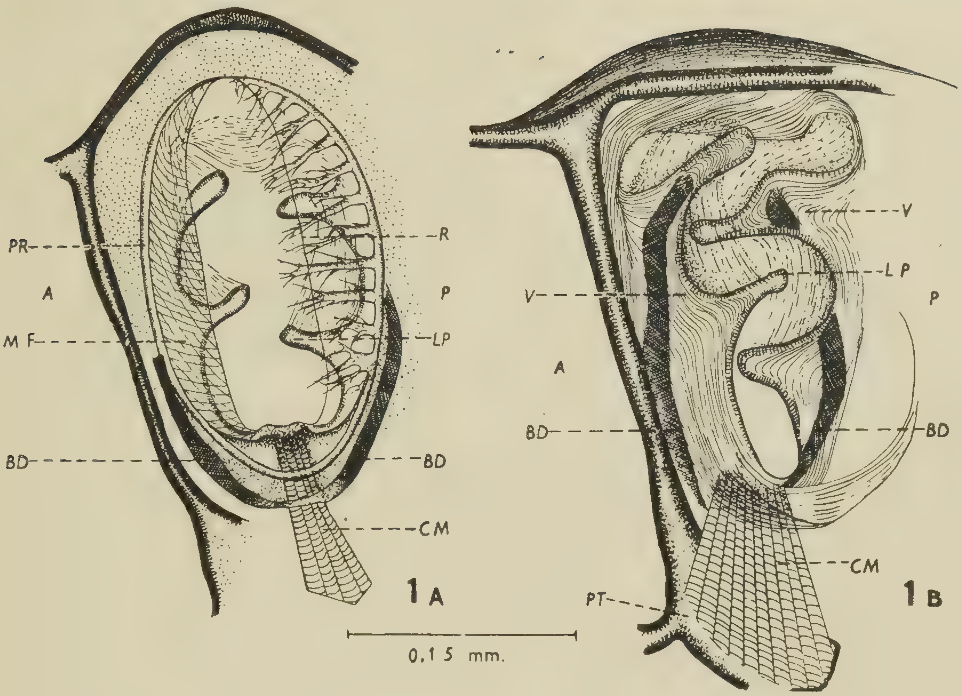
FIG. 1A. Posterior thoracic spiracle, external view showing the connection between the different parts of the regulatory apparatus—open.

1B. Posterior thoracic spiracle, internal view showing the lamellae—closed.

FIGS. 2A and 2B. Serial longitudinal sections of the posterior thoracic spiracle, showing the different parts of the regulatory apparatus.

Key to lettering.

A—Anterior: BD—Band: CM—Closing muscle: E—Elastic plate: LP—Lamellae partition: MF—Membranous flap: P—Posterior: PR—Peritreme: PT—Plate: R—Ring: V—Vestibule.


PR
A
MF
BD
R
P
LP
BD
CM
1A
0.15 mm.
V
LP
V
P
A
BD
BD
CM
PT
1B

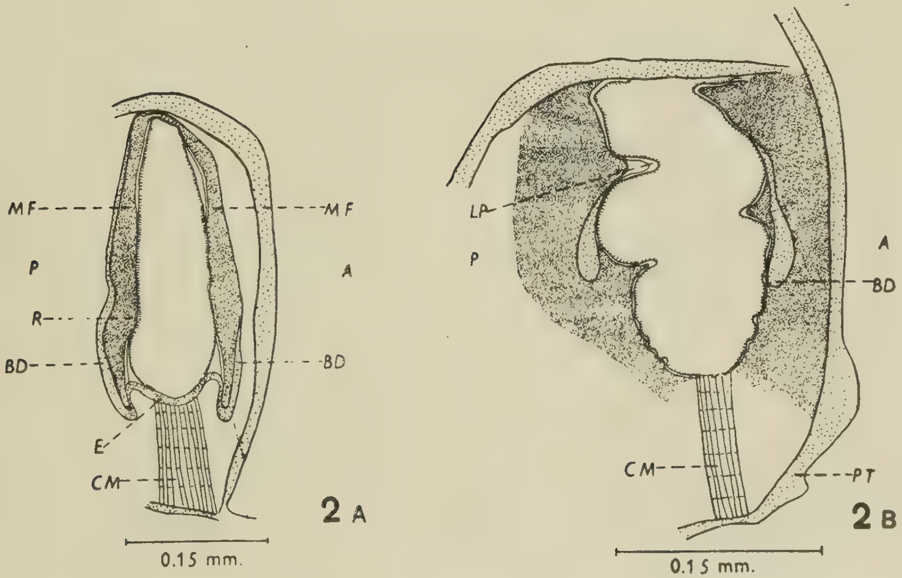

MF
P
R
BD
E
CM
MF
A
BD
2A
0.15 mm.
LP
P
A
BD
CM
PT
2B
0.15 mm.

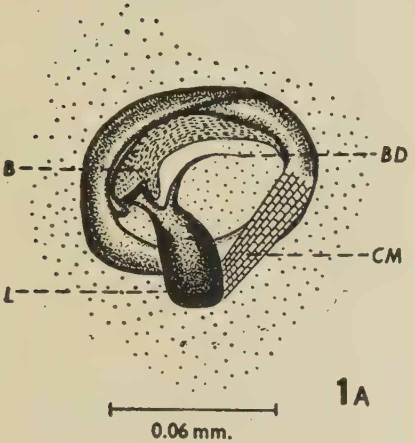
PLATE XVI.

Rhingia campestris (Mg.) and *Syrphus balteatus* (Deg.).

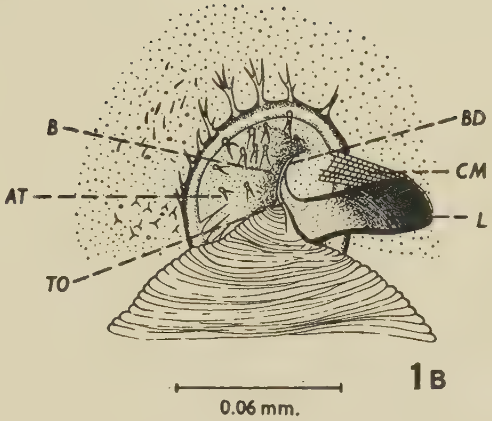
FIG. 1A. Abdominal spiracle of *R. campestris*, internal view, showing the different parts of the regulatory apparatus.
1B. Abdominal spiracle of *R. campestris*, internal view—closed.
2. Anterior thoracic spiracle of *S. balteatus*, internal view—open.
3. Abdominal spiracle of *S. balteatus*, internal view—open.

Key to lettering.

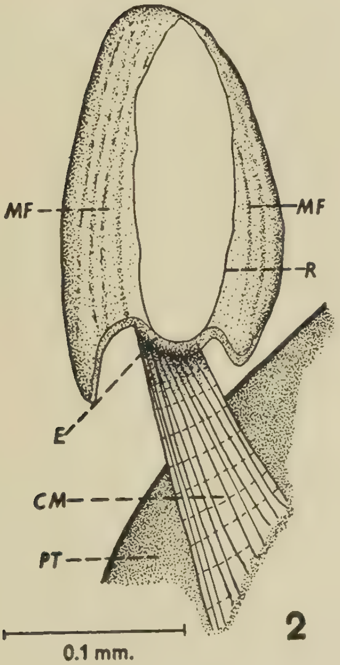
AT—Atrium : B—Bridge : BD—Band : CM—Closing muscle : E—Elastic plate : L—Lever : MF—Membranous flap : PT—Plate : R—Ring : TO—Tracheal opening.


B
BD
CM
L
0.06 mm.

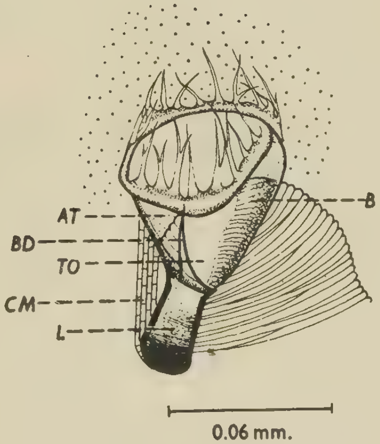
1A


B
BD
CM
AT
L
TO
0.06 mm.

1B


MF
MF
R
E
CM
PT
0.1 mm.

2


B
AT
BD
TO
CM
L
0.06 mm.

3

PLATE XVII.

DROSOPHILIDAE.

Drosophila melanogaster (Auctorum).

FIG. 1. Anterior thoracic spiracle, external view, showing the hairy cover or filter apparatus.

2A. Anterior thoracic spiracle, internal view—open.

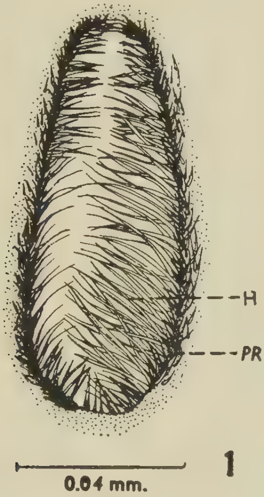
2B. Regulatory apparatus of the anterior thoracic spiracle—closed.

FIGS. 3A and 3B. Abdominal spiracle, internal view—in the open and closed positions.

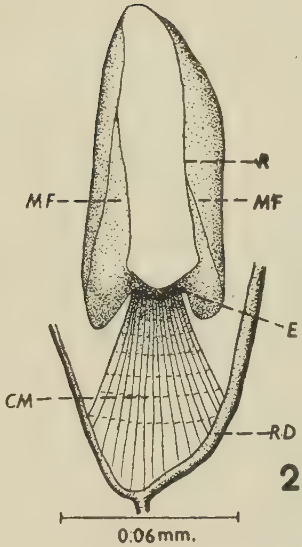
4A and 4B. Serial longitudinal sections of an abdominal spiracle showing the different parts of the regulatory apparatus and their connection with the spiral rings of the atrium.

Key to lettering.

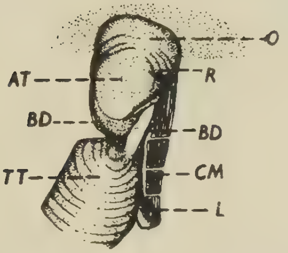
AT—Atrium : BD—Band : CM—Closing muscle : E—Elastic plate : H—Hairs : K—Knob-like process : L—Lever : MF—Membranous flap : O—Spiracular opening : PR—Peritreme : R—Ring : RD—Ridge : TT—Tracheal tube.



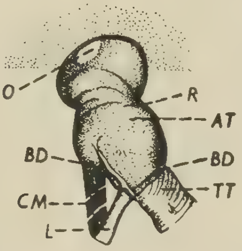
1


R
MF
MF
E
CM
RD
0.06 mm.

2A

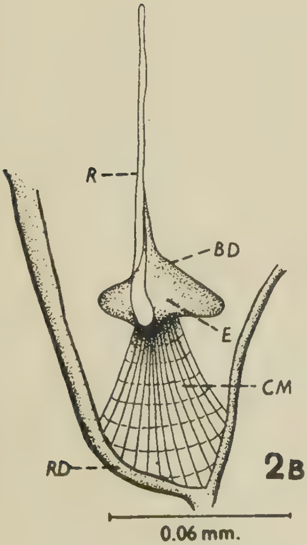

O
AT
R
BD
BD
TT
CM
L

3A

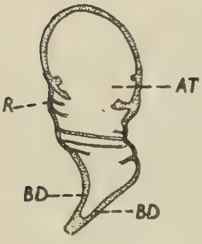

O
R
AT
BD
BD
TT
CM
L

3B

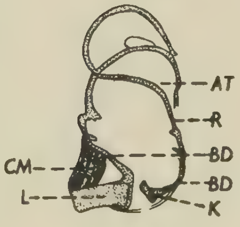
0.05 mm.


R
BD
E
CM
RD
0.06 mm.

2B



4A


AT
R
BD
CM
BD
L
K

4B

0.05 mm.

PLATE XVIII.

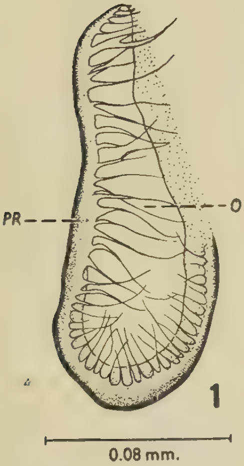
ORTALIDAE.

Platystoma seminationis (Fab.).

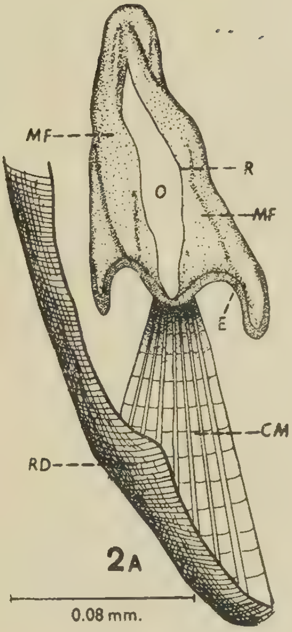
FIG. 1. Anterior thoracic spiracle, external view—showing the hairy cover or filter apparatus.
2A. Anterior thoracic spiracle, internal view—open.
2B. Anterior thoracic spiracle, internal view—closed.
3. Posterior thoracic spiracle, internal view—open.
4. Abdominal spiracle, internal view—open.

Key to lettering.

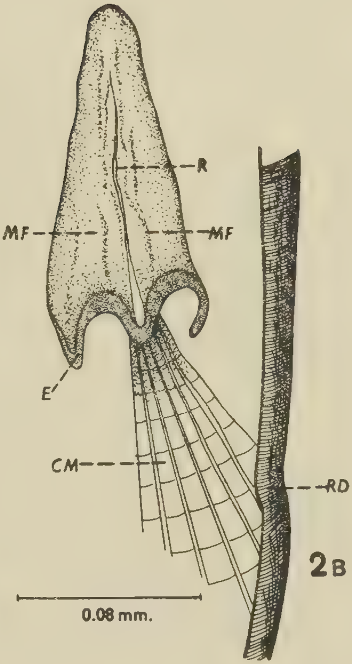
AT—Atrium: BD—Band: CM—Closing muscle: E—Elastic plate: L—Lever: MF—Membranous flap: O—Spiracular opening: PR—Peritreme: R—Ring: RD—Ridge: TT—Tracheal tube.


PR
O
0.08 mm.

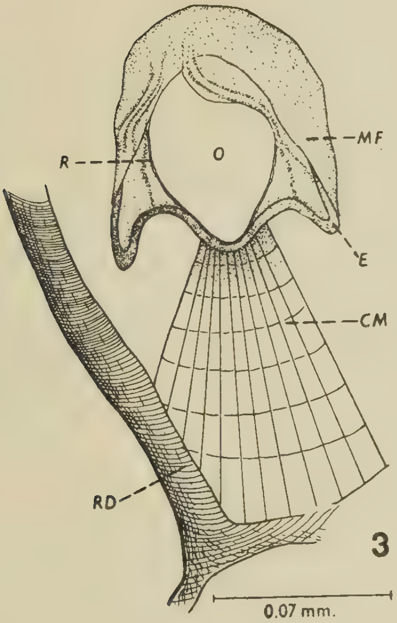
1


MF
R
O
MF
E
CM
RD
0.08 mm.

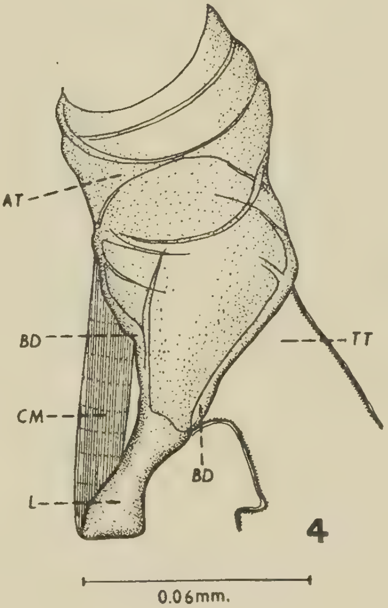
2A


R
MF
MF
E
CM
RD
0.08 mm.

2B


R
O
MF
E
CM
RD
0.07 mm.

3


AT
BD
TT
CM
BD
L
0.06mm.

4

PLATE XIX.

CORDYLURIDAE.

Scatophaga stercoraria L.

FIG. 1. Anterior thoracic spiracle, internal view—open.
2. Posterior thoracic spiracle, external view—showing the hairy cover or filter apparatus.
3. Posterior thoracic spiracle, internal view—open.

FIGS. 4A and 4B. Abdominal spiracle, internal view—open and closed.

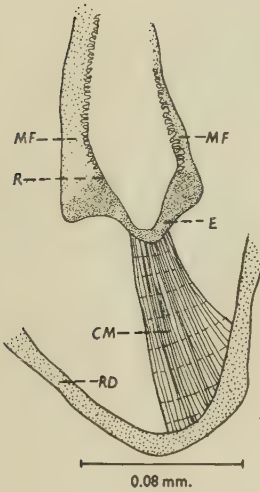
BORBORIDAE.

Sphaerocera subsultans (L.).

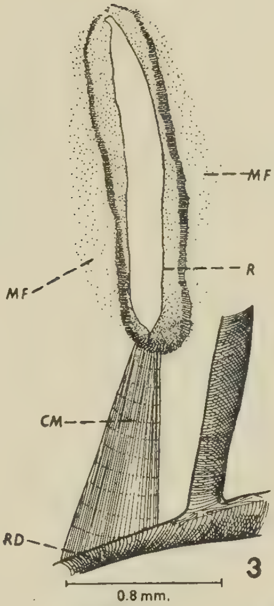
FIG. 5. Posterior thoracic spiracle, internal view—open.

Key to lettering.

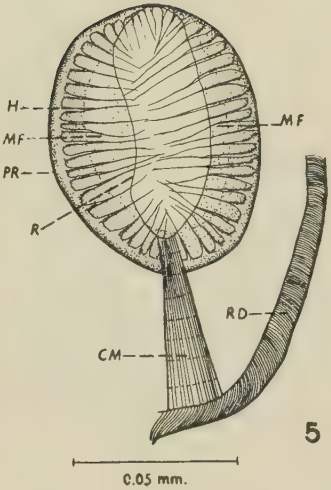
AT—Atrium : CM—Closing muscle : E—Elastic plate : H—Hairs : L—Lever : MF—Membranous flap : PR—Peritreme : R—Ring : RD—Ridge.


MF
MF
R
E
CM
RD
0.08 mm.

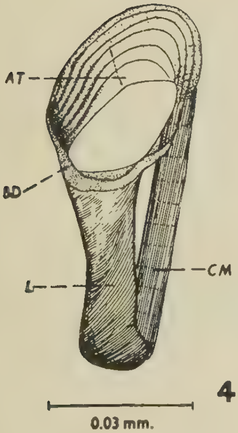
1


MF
MF
R
CM
RD
0.8 mm.

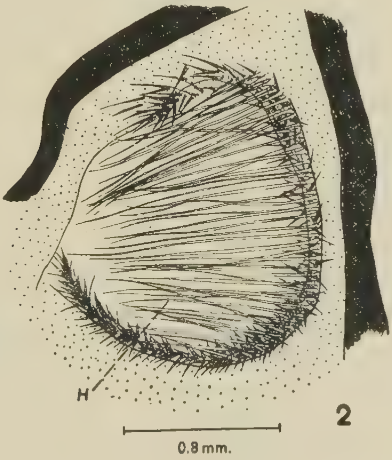
3


H
MF
PR
R
MF
RD
CM
0.05 mm.

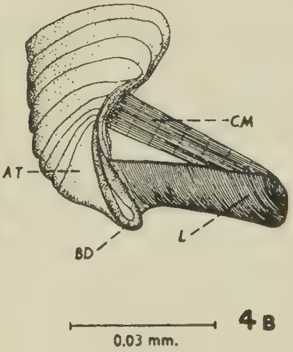
5


AT
BD
L
CM
0.03 mm.

4 A


H
0.8 mm.

2


CM
AT
BD
L
0.03 mm.

4 B

PLATE XX.

Calliphora erythrocephala Macq.

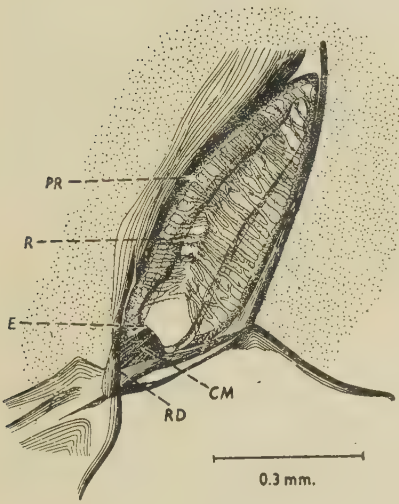
FIG. 1. Anterior thoracic spiracle, external view—open.
2. Posterior thoracic spiracle, external view—open.
3. Regulatory apparatus of the posterior thoracic spiracle (dissected out)—open.
4. Regulatory apparatus of the posterior thoracic spiracle (seen from inside the thorax)—closed.

Musca domestica L.

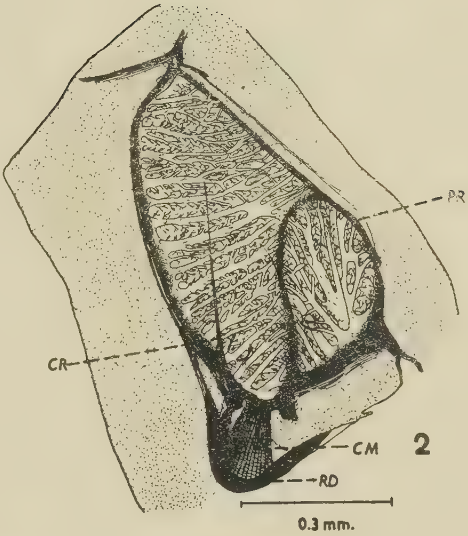
FIG. 5. Thoracic spiracle, internal view—open.

Key to lettering.

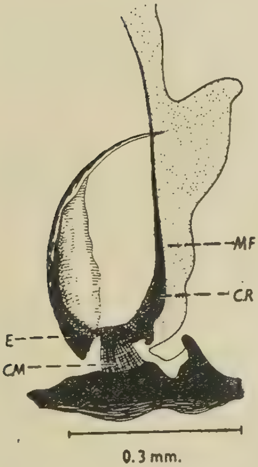
CM—Closing muscle; CR—Calliper: E—Elastic plate: MF—Membranous flap: PR—Peritreme: R—Ring: RD—Ridge.


PR
R
E
CM
RD
0.3 mm.

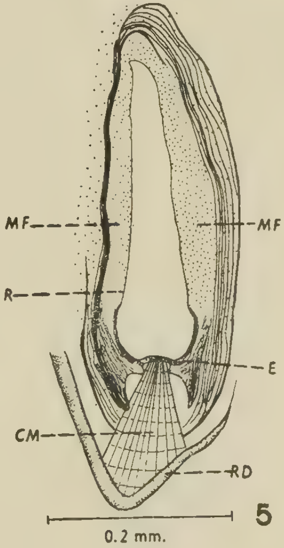
1


PR
CR
CM
RD
0.3 mm.

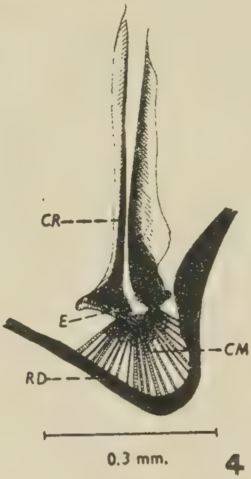
2


MF
CR
E
CM
0.3 mm.

3


MF
MF
R
E
CM
RD
0.2 mm.

5


CR
E
CM
RD
0.3 mm.

4

PLATE XXI.

TACHINIDAE.

Calliphora erythrocephala Macq.

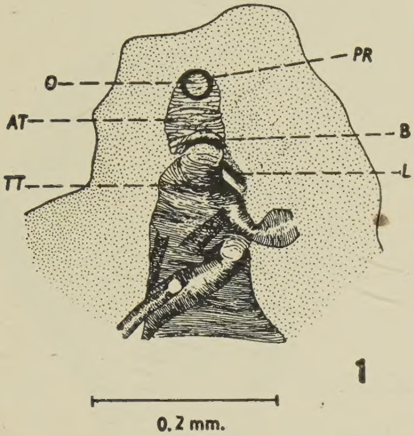
FIG. 1. Abdominal spiracle, external view.
2. Abdominal spiracle, internal view—open.
FIGS. 3A and B. Serial transverse sections at the level of the regulatory apparatus showing the parts of the latter.

Musca domestica L.

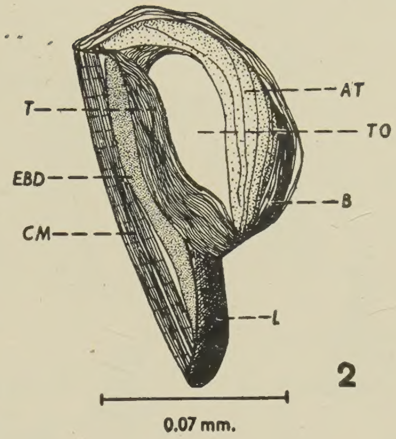
FIG. 4. Abdominal spiracle, transverse section at the level of the regulatory apparatus—open.

Key to lettering.

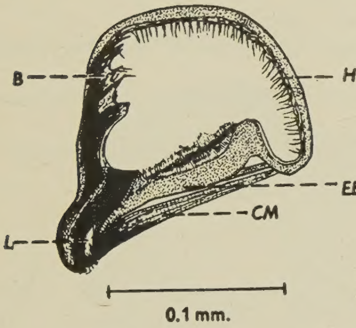
AT—Atrium : B—Bridge : CM—Closing muscle : EBD—Elastic band : H—Hairs : L—Lever : O—Spiracular opening : PR—Peritreme : TO—Tracheal opening : T—Taenidia : TT—Tracheal tube.


PR
O
AT
B
TT
L
0.2 mm.

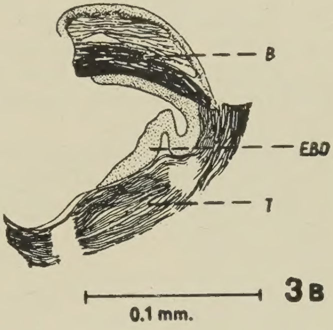
1


AT
T
TO
EBD
B
CM
L
0.07 mm.

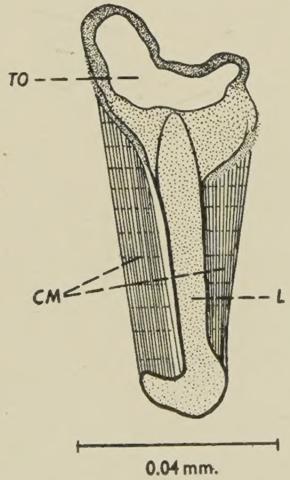
2


B
H
EBD
CM
L
0.1 mm.

3A


B
EBD
T
0.1 mm.

3B


TO
CM
L
0.04 mm.

4

PLATE XXII.

HIPPOBOSCIDAE.

Melophagus ovinus (L.).

FIG. 1. Anterior thoracic spiracle, internal view—open.

FIGS. 2A and B. Serial transverse section through the regulatory thoracic spiracle.

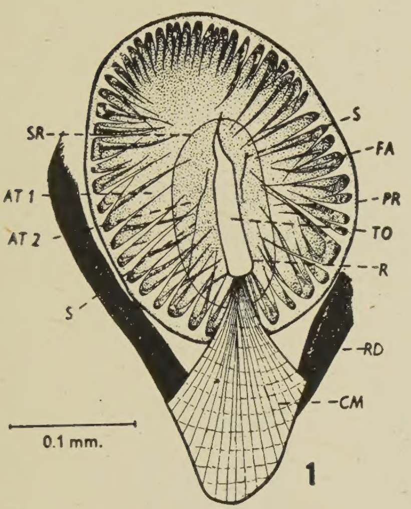
FIG. 3. Abdominal spiracle, inner view—open.

4. Transverse section through the regulatory apparatus of an abdominal spiracle—open.

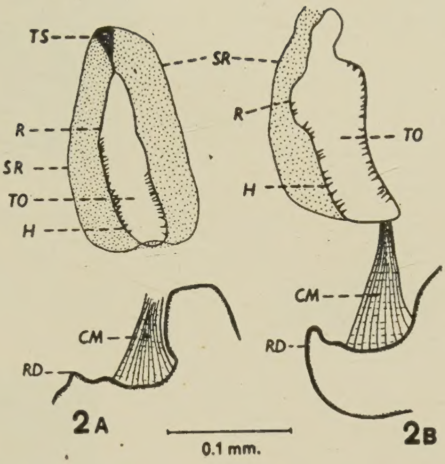
FIGS. 5A and B. Serial longitudinal sections through the regulatory apparatus of an abdominal spiracle—closed.

Key to lettering.

AT—Atrium : AT_1—First atrial division : AT_2—Second atrial division : BD—Band : CM—Closing muscle : EF—Elastic fibres : FA—Filter apparatus : H—Hairs : L—Lever : PR—Peritreme : R—Ring : RD—Ridge : S—Cuticular strands : SR—Supporting ring : TO—Tracheal opening : TS—Triangular sclerotised plate : TT—Tracheal tube.

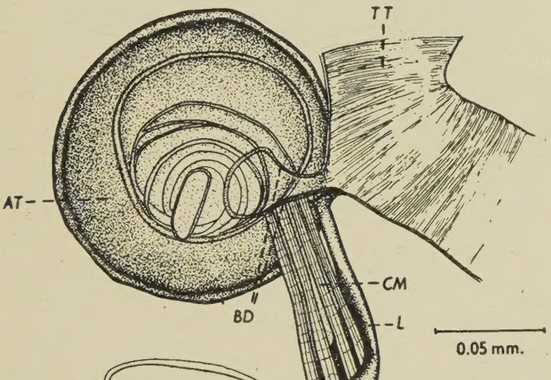

SR
AT 1
AT 2
S
S
FA
PR
TO
R
RD
CM
0.1 mm.

1

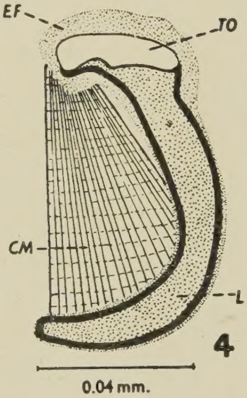

TS
SR
R
SR
TO
H
CM
RD
0.1 mm.
R
TO
H
CM
RD

2A

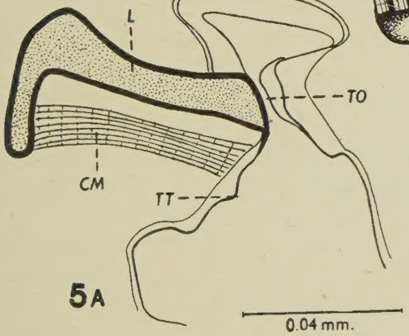
2B


TT
AT
CM
L
BD
0.05 mm.

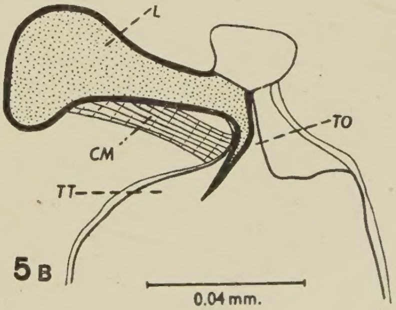
3


EF
TO
CM
L
0.04 mm.

4


L
TO
CM
TT
0.04 mm.

5A


L
TO
CM
TT
0.04 mm.

5B